



PHD

Analysis of Association-Derived Animal Social Networks

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ANALYSIS OF ASSOCIATION-DERIVED ANIMAL SOCIAL NETWORKS

submitted by

Elaine Miranda Bettaney

for the degree of Doctor of Philosophy

of the

University of Bath

Department of Physics

August 2014

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Signed of behalf of the Faculty of Science

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Finally thanks to the University of Bath for providing the funding which enabled me to complete this PhD.

Declaration

None of the work in this thesis claimed to be my own has been incorporated from a submission for any other degree. The biological datasets were collected by others. D.P. Croft (University of Exeter) and co-workers collected the Trinidadian guppy data discussed in chapters 5 & 6. The New Caledonian crow study discussed in chapter 7 was conceived by C. Rutz (University of St Andrews) and fieldwork was led by C. Rutz, J. St-Clair (University of St Andrews) and Z. Burns (University of Oxford). A separate and complementary analysis of the crow dataset was included in the DPhil thesis of Z. Burns. Encounternet technology used in this study was developed by J. Burt and B. Otis (both University of Washington). Save for this, the work is my own.

Abstract

The social structure of animal societies can be instrumental to the evolution and maintenance of animal behaviour. Animal social networks (ASNs) provide a framework with which to visualise, quantify and analyse animals' social structure.

The work in this thesis incorporates two areas of ASN research. The first area is the analysis of sparse group-derived data. Observation of group memberships is a widely used method to uncover social preferences. Here this method is used to probe the social structure of a population of Trinidadian guppies (*Poecilia reticulata*). The network is analysed to ascertain if genetic relatedness may play a role in governing social structure. The bright colourings of male fish are also analysed to see if colour influences male-male associations. The guppy study provided motivation for an investigation into association indices for group-derived data. Existing indices are evaluated using a simulated dataset and a new index is proposed.

The second part of this thesis contributes to a new and exciting trend in ASNs in which complete records of animal associations are obtained enabling temporal network analysis to be used. This is applied to a population of New Caledonian crows (*Corvus moneduloides*) which are of interest particularly for their ability to manufacture and use tools for foraging. Emulations of information flow through the network are used to assess the network's information flow potential. A network structure in which information can spread rapidly could indicate that crows can potentially learn tool use skills from their peers.

Part I

Introduction

Chapter 1

Introduction

An animal's social environment consists of all other animals with which it interacts, and the size of this environment varies greatly not only between species but also between individuals in a population. The mixing of animals within a population is not homogeneous and this variation can have significant consequences for the fitness of the individual and for social dynamics (Sih et al. 2009).

A framework for characterising animal societies was put forward by Hinde (1976). Hinde categorised the society into three levels: interactions, relationships and structure. Interactions occur between two individuals and may be affiliative (e.g. grooming or playing), antagonistic (e.g. fighting), co-operative (e.g. social foraging) or sexual to name but a few. They usually last for a short period of time. The accumulation of many interactions between a pair of individuals constitutes a relationship. The relationship is characterised by the type, frequency and quality of the interactions. The final level of society is structure. This is an overview of all relationships which exist between individuals in a population and is characterised by the 'content, quality and patterning' (Hinde 1976) of the relationships.

The structure of a society can be conveniently visualised as a network, although Hinde did not utilise this. A network consists of a set of nodes connected by a set of edges (see Figure 1.1). For an animal social network (ASN) the nodes represent individual animals and the edges associations or interactions between them. The amount of literature available on network science has increased dramatically over

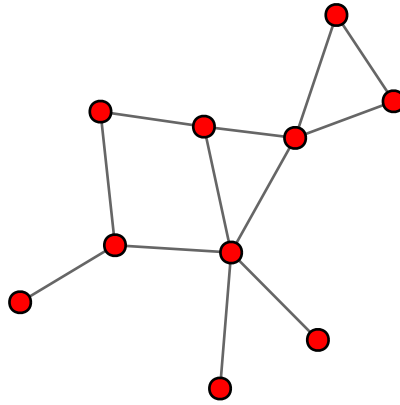


Figure 1.1: *A network with 10 nodes and 12 edges.*

the last 20 years (Carrington et al. 2005) and has been widely used across many disciplines including mathematics, physics, biology, engineering and chemistry (Newman et al. 2006). Social networks were first used by social scientists to describe the social structure among humans (Newman et al. 2006) and have only more recently been applied to animal societies. A brief history of network science will be given in Chapter 2.

Animal Social Network Analysis (ASNA) provides an analytical framework with which to quantify the social structure of a population (Sih et al. 2009). Observational data of interactions between animals can be combined to build a social network which can reveal the underlying structure. Various network measures have been developed which describe the structure mathematically and help differentiate between different animals' network positions. The network structure may be used in conjunction with other information about the individuals to uncover governing principles of organisation for example by age, sex or blood relation (Hinde 1976). All three of these traits together with others will be investigated in this thesis.

Although Hinde's framework is based on interactions between animals as being observable events, important relationships can exist between animals which are based solely on associations (Whitehead 2008a). Animals may be associating without performing any observable interactions and so indisputable evidence of association may be impossible to come by. Instead associations are inferred, usually by some measure of spatial proximity or observations of synchronous behaviour (Whitehead 2008a). This inferential nature of associations creates

uncertainty when analysing association data and repeated observations must be used in order to increase confidence in the results.

Although there are difficulties involved in using associative data, they often play an important role in probing animal social structure (Croft et al. 2008). This could be because observations of interactions are unavailable but equally because associations may be informative when asking the question ‘who is friends with whom?’ (Whitehead 2008a). The work in this thesis analyses associative data collected from two species, the Trinidadian guppy (*Poecilia reticulata*) (Ch. 5 & 6) and the New Caledonian crow (*Corvus moneduloides*) (Ch. 7).

1.1 Why social network analysis strengthens the study of animal societies

SNA is a relatively new technique to be applied to animal societies but already it has proven versatile having been used in the study of a wide variety of animals including insects (Blonder and Dornhaus 2011, Naug 2008), fish (Croft et al. 2004b, Pike et al. 2008), birds (Psorakis et al. 2012, Aplin et al. 2012), reptiles (Godfrey et al. 2012), ungulates (Cross et al. 2005, Gero et al. 2013, Gygax et al. 2010, de Silva et al. 2011), rodents (Nanayakkara and Blumstein 2010), carnivora (Drewe et al. 2009, Hirsch et al. 2013) and primates (Flack et al. 2005, Pepper et al. 1999). The simple framework of a network allows all types of animal social structures to be visualised and characterised through the use of network measures (see Ch. 3).

SNA is a particularly useful tool because the social structure of an animal society influences many important areas of behavioural biology (see Krause et al. 2007, Wey et al. 2008 and Sih et al. 2009 for comprehensive reviews). SNA can provide useful insights into topics such as mate choice, sexual selection, co-operation, social learning and information flow (Sih et al. 2009) which other methods of analysis may overlook. In the case of mate choice, Sih et al. (2009) points out that when a male chooses a female mate, it is not only the selection of available females which makes a difference, but also how many mate choices the preferred female has. This ‘indirect’ effect, the number of network neighbours my network neighbours have, is especially suited to the network approach as SNA provides a

description of the way in which pairwise relationships in a society link together and also describes the topology of the network formed.

SNA can be used to study the mechanisms and evolution of animal behaviour and co-operation. Behavioural studies seek to find links between behavioural traits and network position sometimes with a view to explaining variation in individual fitness or reproductive success. Examples of such studies include Wey and Blumstein (2012) (marmots), Croft et al. (2009b) (guppies), Godfrey et al. (2012) (lizards) and Pike et al. 2008 (sticklebacks). The social conditions under which co-operation occurs can be probed using SNA. This is a theme in work by Croft and co-workers (from 2004 and ongoing) to which Chapter 5 is a contribution. The presence or absence of persistent relationships can be found and the quality of such relationships determined (Croft et al. 2004b). Underlying rules governing the structure of the network may be discovered and these can be related back to the conditions required for co-operation (Croft et al. 2006).

A more recent trend, facilitated by advances in technology, is the use of temporal data for animal social networks (Krause et al. 2011, Ryder et al. 2012). This use of timestamped association or interaction data enables the study of information flow which in turn can inform subjects such as social learning (e.g. Kopps and Sherwin 2012) and the transmission of disease (e.g. Hamede et al. 2009). It is possible to create models of information flow through static networks (e.g. Aplin et al. 2012)) and these are already an improvement on non-network based models of information flow, since homogeneity of associations is not assumed. However timestamped data allows analysis to go a step further and see how the time ordering of associations or interactions affects information flow. Part III of this thesis analyses timestamped proximity data in the context of social learning.

SNA is a powerful tool allowing the study of many diverse topics using a single framework (Krause et al. 2009) however it is not without its difficulties. The difficulties largely arise in two areas. Firstly, traditional statistical methods assume independence of data points whereas the interconnected nature of network data means that this assumption is not valid. Secondly, when dealing with observational data of animals many uncertainties or biases may exist in the data which create an added layer of difficulty in the analyses. Network analysis did not evolve with behavioural ecologists in mind and so there is now a growing literature aimed at resolving the difficulties particular to animal studies. This

thesis aims to contribute to the expansion and refinement of analytical methods used in studies of animal social networks.

1.2 Thesis overview

This thesis is arranged into four parts. Part I is an introduction summarising the key ideas contained in this thesis. In Chapter 2 I give an introduction to the history of network theory and describe the technical details of calculating network measures. Chapter 3 concludes this introduction section by outlining the methods used in a typical ASN study.

Parts II and III comprise the two main analysis sections of this thesis. Part II is focussed on analysing group derived data. This is where repeated observations of group memberships are used to infer associations. Chapter 4 provides an introduction to this topic describing how a typical study may be executed from data collection through to analyses and testing hypotheses. This provides background knowledge for a piece of analysis on the social network of the Trinidadian guppy which is presented in Chapter 5.

The work in Chapter 5 investigates whether relatedness could be a factor contributing to the social structure of the guppies. No evidence was found for this. In a separate piece of work using the same guppy set male-male associations are analysed to see if they are influenced by male body colourings. The results suggested that this could be the case.

Following on from guppy study Chapter 6 explores the topic of association indices. Studies with sparse datasets, often the case for group derived data, employ AIs to counteract biases introduced at the sampling stage. However AIs bring their own often unknown biases. Chapter 6 investigates the bias present in association indices when used for open populations where animals are free to leave the study area.

In Part III the focus shifts from static to temporal networks. Chapter 7 studies a temporal association network of a population of New Caledonian crows. This work is enabled by the Encounternet system which consists of bird-mounted

transceivers that create timestamped logs of proximity between birds. This rich dataset is a stark contrast to the sparse manually collected data of Chapter 5. Emulations are run of information flow through the network which assess the potential for information to spread through the network. The emulations showed that if a piece of information takes on average 5 min to be transferred from one crow to another then information can spread to up to 6 other crows during one day. New Caledonian crows use and manufacture tools for foraging purposes and this study provides an insight into whether it is possible for tool related activities to be learnt from peers.

Part IV concludes by discussing the relevance of the work in this thesis to the possible future directions of ASN analysis.

Chapter 2

Network theory

Networks can be found everywhere. From infrastructure such as roads or railways, to biological systems such as neural networks or the vascular system, social networks of human societies and information networks such as the World Wide Web. These examples and many more can all be conceptualised in terms of a network, a collection of *nodes* connected by a set of *edges*. The field of network science is contributed to by mathematicians, physicists, computer scientists, sociologists, biologists and others, reflecting its wide applicability (Newman et al. 2006).

2.1 History of network science

In 1736 Leonard Euler became interested in a popular problem of the time known as the Königsberg Bridge Problem (Newman et al. 2006). The city of Königsberg was bisected by a river in which there were two large islands. Seven bridges linked the four separate land masses (Fig. 2.1a). The question was whether it was possible to walk across all seven bridges using each bridge only once. To solve this Euler converted the problem into what we now know as a network. Each land mass was represented by a node and edges between the nodes represented the bridges (Fig. 2.1b). Euler proved that for such a path on a network to exist, there can be at most two nodes which have an odd number of edges attached to them (a quantity known as node *degree*). This is because apart from the start and

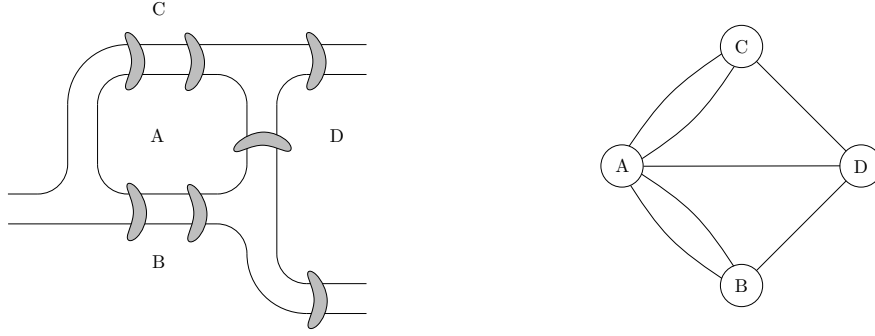


Figure 2.1: *The Königsberg Bridge Problem adapted from Euler (1741). a) The layout of the city of Königsberg with seven bridges connecting the four land masses A, B, C & D. b) A network representation of the problem where each node represents a land mass and edges represent the bridges.*

finish nodes, a path must enter and leave each node on different edges meaning the degree must be even. In the network of Königsberg bridges all four nodes have an odd degree and so a path using each bridge only once does not exist.

Euler's proof is considered by many to be the first theorem in the field of network science (Newman et al. 2006). Since then mathematicians have built on this to create what is known as *graph theory*, the mathematical language for describing the properties of networks. Physicists considered the case where the number of nodes is large (*n is large*) and drew from the fields of statistical mechanics and thermodynamics in order to describe the statistical properties of large networks. In this way network science was mainly advanced as a theoretical framework which was not applied to empirical data.

In the mid 1930s sociologists began to use the construct of a network to describe the social relationships between people and the field of Human Social Network Analysis (HSNA) developed (Newman et al. 2006, Wasserman and Galaskiewicz 1994, Carrington et al. 2005). HSNA used relatively small sets of empirical data often collected via surveys or questionnaires (Carrington et al. 2005, Newman et al. 2006). Such data is far from the realm of *n is large* and so sociologists developed a new area of network science to accommodate this by adapting some concepts from graph theory (Newman et al. 2006).

In the last 20 years, due to computerisation, large data sets have become increasingly available and these have given scientists from a range of disciplines the

opportunity to apply network theory to the real world. Accordingly, the interest in network science has increased rapidly. Physicists have now been able to test the applicability of theoretical models such as ‘small-world’ (Watts and Strogatz 1998) and ‘scale-free’ (Barabási and Albert 1999) to real world data sets such as the world-wide airport network or the scientific collaboration network (Barrat et al. 2004).

Another branch of network science which began in the mid 1900s is network dynamics. One component of this is how a graph may grow or evolve over time (Erdős and Rényi 1961). A second element of dynamics is how information or disease may propagate through the network (Solomonoff and Rapoport 1951). Recently there has been a move to create a distinction between these two examples (Gross and Blasius 2008, Sih and Wey 2013). The former is an example of dynamics *of* networks where the topology of the network is a dynamical system, in other words edges and/or nodes can appear and disappear over time (Gross and Blasius 2008). The latter is an example of dynamics *on* networks, the network topology is fixed and dynamical processes happen on them changing the state of the nodes (Gross and Blasius 2008).

At the intersection between dynamics *of* networks and dynamics *on* networks is the field of *adaptive* networks. In an adaptive network the dynamics *on* the network affects the dynamics *of* the network creating a feedback loop (Gross and Blasius 2008). One example of this is that of opinion formation (e.g. Gil and Zanette 2006, Holme and Newman 2006). A social network can be constructed where the state of each node can reflect the political opinion of a person. People may choose to cease associations with other people of opposing political opinion and form new associations with people of matching political opinion. Alternatively people may change their own political opinion to match that of their network neighbour’s. Such a network will evolve according to the dynamics of the processes occurring on the nodes and so is said to be an adaptive network.

This thesis is concerned with two types of network. Firstly a static network is used to represent the social structure of a population of Trinidadian guppies (Ch. 5). Secondly, time-stamped data are used to create a temporal network – a dynamic network where edges exist during specified time intervals (Ch. 7). I will also consider a dynamical process played out on the temporal network. In the remainder of this chapter I will introduce some basic terminology and methods

for describing both types of network.

2.2 Introduction to static networks

Networks exist in an extensive variety of sizes and topologies. In order to quantify the characteristics of the different topologies mathematicians have defined a range of measures, some of which will be presented here. Networks can be categorised according to the type of edge they contain. Networks may be directed, meaning each edge has a *from* node and a *to* node, or undirected, where there is no differentiation between the two endpoints of an edge. Networks may also be weighted or binary. In weighted networks each edge may have a numerical weight assigned to it whereas in a binary network edges are either present or absent.

Three examples of different network topologies are shown in Figure 2.2. In Figure 2.2a the network is complete meaning all possible edges exist. In this case the network is symmetrical, all nodes are identical in their position in the network. Figure 2.2b shows an example of an Erdos-Rényi random graph (Erdős and Rényi 1961) which is perhaps the most widely known random graph model. A graph $G(n, m)$ of n nodes and m edges is chosen at random from the set of all possible $G(n, m)$. In the example shown in the figure, $n = 40$ and $m = 50$. Figure 2.2c shows a directed ‘tree’. Each node, apart from the ‘root’ and ‘leaf’ nodes, has one incoming edge and 3 outgoing edges.

To illustrate some simple network measures, I have created a small toy network (Fig. 2.3). To avoid complication the network is undirected and binary. The network contains 5 nodes and 5 edges which gives it a network edge density (the fraction of all possible edges which are present) of 0.5. Networks are often characterised by node and network measures, the former being specific to each node and the latter a network wide property often an average over all nodes of a node based measure. A range of node measures has been calculated for the toy network and is also shown in Figure 2.3. I will now describe each of them in turn.

Perhaps the simplest node measure is node degree often denoted k_i (Freeman 1978–1979). This is simply the number of edges which are connected to a node. Degree is a local measure of network structure since it only considers a node’s

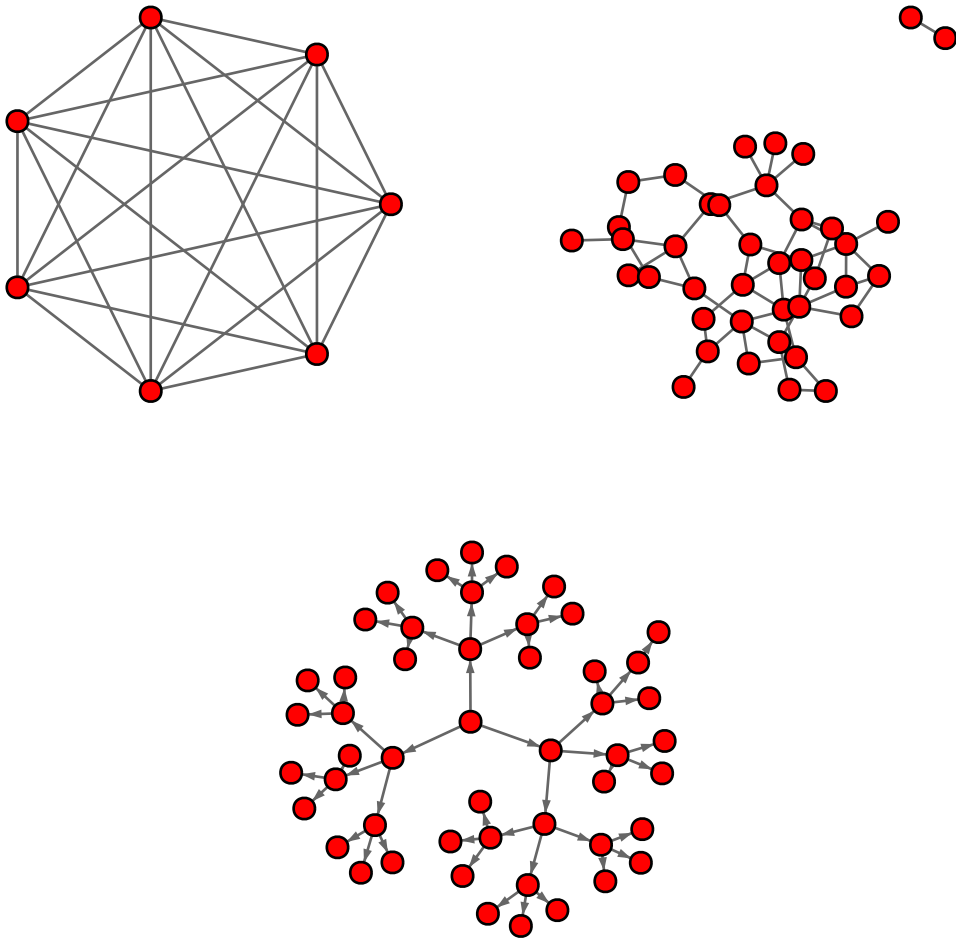
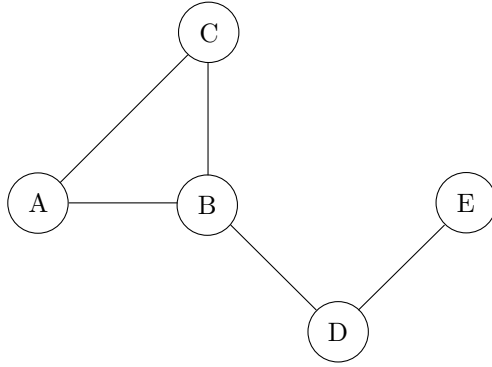


Figure 2.2: *Examples of different network topologies. a) A complete network. All possible edges exist. b) A random network based on Erdős and Rényi (1961) with 40 nodes and 50 edges. The network is selected at random from the collection of all possible networks with 40 nodes and 50 edges. This network contains two components, one containing 38 nodes and the other 2. c) A tree. Nodes form a hierarchy with each node having 3 ‘child’ nodes.*



| Node | k_i | L_i | B_i | C_i |
|----------|-------|-------|-------|-------|
| <i>A</i> | 2 | 2 | 0 | 1 |
| <i>B</i> | 3 | 1.25 | 4 | 0.33 |
| <i>C</i> | 2 | 1.75 | 0 | 1 |
| <i>D</i> | 2 | 1.5 | 3 | 0 |
| <i>E</i> | 1 | 2.25 | 0 | 0 |

Figure 2.3: A toy network together with the values of some node based measures.

immediate neighbours. In the toy network *B* has the largest degree of 3 and *E* the smallest of 1.

An important network concept is the idea of a path. A path is a sequence of edges which connect two nodes (the definition of a path allows each edge to be used only once compared with a *walk* or *trail* where edges may be used multiple times). For example in the toy network nodes *A* and *D* are connected by the path $\{A, B, D\}$. In general there may be many paths connecting a given pair of nodes (e.g. the path $\{A, C, B, D\}$ also connects *A* with *D*) so it is more common to talk instead about the shortest path. The length of a path is the number of edges it uses and is denoted d_{ij} . Two nodes are connected if a path exists between them and a component is formally defined as a group of nodes which are all connected.

Measures of node centrality describe a node's position in relation to the rest of the network. A simple measure of node centrality can be defined from the concept of a path. The average of the shortest paths from a node to each other node, L_i , is sometimes called *farness* (Croft et al. 2008). For a network containing n nodes farness is defined as

$$L_i = \frac{1}{n-1} \sum_{j=1}^n d_{ij},$$

where

$$d_{ii} \equiv 0$$

and quantifies how closely connected each node is to each other node. L_i will be small if node i is on average close to all other nodes and large if it is far away. In Figure 2.3 *B* has the lowest farness and so by this measure is the most central node in the network. A similar measure *closeness centrality* measures the inverse of this (Newman 2010).

How far away a node is from all other nodes is just one aspect of node centrality. Another node centrality measure also based on the idea of a path is *betweenness* (B_i) (Freeman 1978–1979). The betweenness of node i is the number of shortest paths between nodes other than i which pass through i . Betweenness is concerned with how important a node is in connecting different parts of the network, a concept which is important for example in the rail or road network. In the toy network the shortest paths from $A \rightarrow E$, $B \rightarrow E$ and $C \rightarrow E$ all pass through D and so D 's betweenness is 3.

The final concept to be mentioned here is clustering coefficient (C_i). This is a local measure of how ‘clique-ish’ the network is around each node or in other words ‘are my friends also friends with each other’. The clustering coefficient of node i is the number of edges existing between i 's neighbours (i 's neighbourhood) divided by the total number of possible edges in i 's neighbourhood. Node i has k_i neighbours so there are $\frac{1}{2}k_i(k_i - 1)$ possible edges between its neighbours. If there are w edges between i 's neighbours then

$$C_i = \frac{2w}{k_i(k_i - 1)}.$$

These measures together with many others help quantify the structure of networks. Some measures have been generalised for use with weighted and or directed networks (Barrat et al. 2004, Newman 2001). For example *node strength* is the weighted network counterpart of degree and is calculated by summing the weights of all edges attached to a given node (Barrat et al. 2004). As pointed out in Opsahl et al. (2010) however, incorporating weights can change the meaning of a measure. A node may have a large node strength by summing over a small number of edges with large weights or by summing over many edges with small weights. Similarly, a weighted path length may be long for either of the same two reasons. The relative importance of the number of edges versus the edge weights may differ depending on the purpose of the analysis. Opsahl et al. (2010) suggests using a tuneable parameter in order to adjust the balance between number of edges and edge weights to give each the desired importance.

2.2.1 Dependence

The fundamental issue that makes network data harder to analyse than non-network data is that of dependence. Each edge links two nodes and in doing so affects the properties of both nodes. It is easy to see for example how the degree of one node is connected with the degree of all the node's network neighbours. However it is not just local node measures which are correlated. Network wide node measures such as betweenness rely on paths between all network nodes. A shortest path between nodes i and j can pass through any number of intermediate nodes and this same path will be used in the calculation of betweenness for each of the intermediate nodes. Thus the betweenness values of all nodes are partially dependent on one another.

Hoff (2003) illustrates some types of dependence using an example of the social network between a class of school children where each child was questioned on whether he liked each other child. Hoff describes three types of dependence which can exist in such data. Firstly within-node dependence which means that the probability of there being an edge from nodes $i \rightarrow j$ is high if we know that there are edges $i \rightarrow k$ for many other k where $k \neq j$ and low if there are few other edges. Secondly reciprocity, meaning that edges $i \rightarrow j$ and $j \rightarrow i$ are positively correlated. A directed network of friendships will often show high reciprocity. In other words, if I think you are my friend, then it is probable that you think I'm your friend too. The third type of dependence is called transitivity. In general terms if child A is friends with child B and child B is friends with child C , then it is likely that A and C will also be friends.

These dependencies as well as many others complicate the analysis of networks. In the following chapter this issue will be explored in the context of animal social networks.

2.3 Introduction to temporal networks

In a temporal network nodes and edges can appear and disappear over time. Here I focus on the subject of temporal edges as temporal nodes can be accounted for by

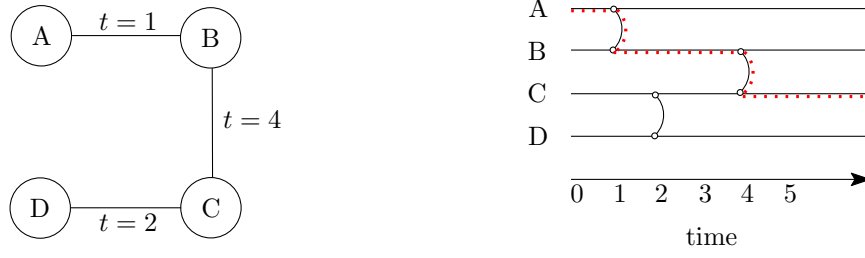


Figure 2.4: a) An example of a temporal network where edges exist instantaneously. The numbers by the edges indicate the times at which the edges exist. b) A timeline visualisation of the contact sequence where each node is represented by a horizontal line extending in time towards the right. A time respecting path exists from $A \rightarrow C$ (indicated by the red dotted line) but not from $C \rightarrow A$.

the presence or absence of edges. Holme and Saramäki (2012) defines two broad types of temporal network, contact sequences and interval graphs. In a contact sequence, each edge only exists either instantaneously or for a negligible duration. A graph may be represented by a series of triplets (i, j, t) where an edge exists between nodes i and j at time t . A contact sequence can be a useful representation for a network of emails sent or conversations on Twitter. In an interval graph, edges are present over a set of periods so each edge can be represented as a quadruplet (i, j, t_n, t'_n) where an edge exists between nodes i and j between times t_n to t'_n . Interval graphs can represent networks such as proximity networks between animals.

Many of the measures used to describe static networks are either no longer applicable or need redefining for temporal networks. Perhaps the most fundamental change when moving to temporal networks is in the idea of a path. In a temporal network a path must respect the time-ordering of the edges (Holme 2005). A path may only exist between two nodes i and j if there is a sequence of edges connecting i to j such that each edge is at a later time than the preceding one. For example in Figure 2.4 an instantaneous edge exists between A and B at $t = 1$ and from B to C at $t = 4$. This means there is a time respecting path from $A \rightarrow C$ $\{(A, B, 1), (B, C, 4)\}$. In contrast to static undirected networks, a path existing from $A \rightarrow C$ does not imply that a path also exists from $C \rightarrow A$, and in the given example it does not as the connection between A and B happens before the connection between B and C .

Another feature of paths on temporal networks is that they are themselves tem-

poral. Their existence depends on the time window over which you look. If in Figure 2.4 you choose a time window $0 \leq t < 3$ then there is no longer a path from $A \rightarrow C$. This dependence of paths on time window definition means that any measure calculated using paths is also a function of the time window.

The changes in the definition of a path mean that there is no longer a well defined concept of a component in temporal graphs. Instead it is replaced with the idea of *reachability* which defines whether nodes can be reached from other nodes via time respecting paths within a given time window. The set of nodes which can be reached from node i is called the *set of influence* of i and the set of nodes from which i can be reached is called i 's *source set* (Holme and Saramäki 2012) (these are referred to as *outdomain* and *indomain* in Ch. 7).

The idea of path length is replaced by *latency*, also called *temporal path length* (Pan and Saramäki 2011). In a temporal network the ‘distance’ between two nodes becomes the time taken to get from one node to the other. The latency $\lambda_{ij}(t)$ is the time taken for the shortest time respecting path starting at node i at time t to reach node j . Plotting latency over time for a contact sequence gives a ‘saw-tooth’ function as the latency is always equal to the time until the first contact in a path plus the time needed to follow the remainder of the path (Fig. 2.5a). The latency therefore decreases linearly until the first contact in the shortest path and then jumps upwards as the initial shortest path ceases to exist and is replaced by a new shortest path starting at a later time.

Latencies on interval graphs are more complicated since both the start and end times of edges must be considered as edges may now overlap in time (Fig. 2.5b). Latency is further complicated if the idea of waiting times is introduced. A path can be made to pause at every node before being allowed to pass to a new node. This can be used to simulate ideas such as incubation periods in disease transmission or time taken to change platforms when travelling by train. In Chapter 7 I consider paths where a finite time τ is taken to cross between nodes and τ is a random variable.

The average latency between two nodes, a measure of how well connected they are during a given time window, is technically found by integrating the saw-tooth latency function over the time window. However this is not easy in practice as latency becomes infinite as soon as the final path disappears. Pan and Saramäki

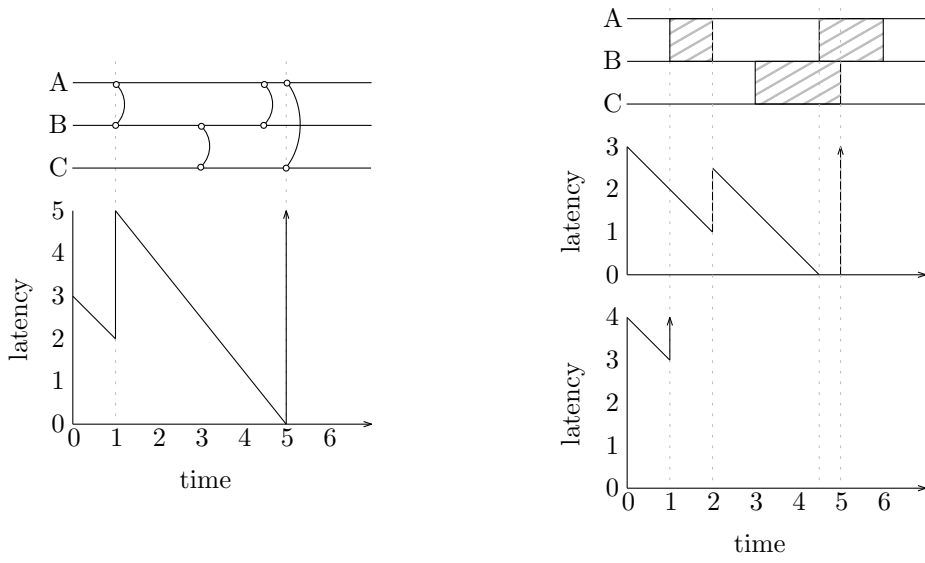


Figure 2.5: a) Latency from $A \rightarrow C$ as a function of time for a contact sequence. Transitions between nodes happen instantaneously when there is an edge present. b) Latency from $A \rightarrow C$ for an interval graph. The upper plot shows the latency if transitions happen instantaneously while in the lower plot, a waiting time of 1 time unit has been introduced so that a path must wait on each node for at least 1 time unit before following an edge to another node. With a waiting time of 1, a path can no longer pass from $A \rightarrow B \rightarrow C$ after $t = 1$ as the overlap between the later two edges in the graph is < 1 .

(2011) suggests that this may be dealt with by applying periodic boundary conditions to the latency so that all paths from nodes i to j repeat with a period equal to the time window. This is done for each pair of nodes separately so that no additional paths between other nodes with lengths longer than the time window are inadvertently created.

Analogous to static networks, centrality measures in temporal networks can be constructed using the idea of time respecting paths. A common example of this is *temporal closeness centrality* (TCC) defined as

$$TCC_i(t) = \frac{n-1}{\sum_{j \neq i} \lambda_{ij}(t)}.$$

This is a measure of how quickly one may reach all other nodes from node i and depends on the time t at which it is measured. It can however be problematic to calculate TCC as $\lambda_{ij}(t)$ is infinite if no time respecting path exists between i and j . This condition is far more restrictive than requiring a static network to be connected because as t advances, fewer and fewer paths remain. A few methods

exist to circumvent this problem including averaging the latencies over time or instead summing the inverse of the latencies (Holme and Saramäki 2012).

As a ‘halfway house’ between static and temporal networks, the time evolution of networks is sometimes studied by creating series of ‘time aggregated’ static networks from temporal ones (Blonder et al. 2012). A time aggregated network can be made by accumulating all edges which appear in a temporal network during a given time window. Having made a static network it can now be analysed with a suite of static network measures which are far simpler to calculate than temporal measures. They can for example make it easy to compare different time periods of a network to see if network properties are changing or remaining constant. Care must be taken when choosing the duration of time windows as different conclusions may be reached depending on the size of the window (Blonder et al. 2012, Caceres and Berger-Wolf 2013). The timescale for which edges exist may be a consideration as it may be advantageous to either pick a time window very large in comparison to this, or a time window comparable to this.

However the time windows are chosen, information will always be lost when time aggregating which could be crucial when studying dynamics *on* the network. In Chapter 7 I study a temporal network both as an interval graph and also as a series of time aggregated static networks. I found that when analysing the flow of information through the network, a dynamic process *on* the network, it was important to retain the full timestamped data as the time ordering of edges is fundamental to the existence of time respecting paths. I also found the approach of time aggregation to be useful for finding basic differences between the data on different days of the study.

Chapter 3

Methods of Animal Social Network Analysis

Analogous to work carried out by social scientists on human social networks (HSNs), animal social network (ASN) studies endeavour to reveal social structure within populations of animals. ASN studies have borrowed many ideas and techniques from HSN studies, for example many network metrics (like those described in Sec. 2.2) originated in the study of HSNs and are now applied to ASNs. The earliest ASN studies came in the field of primatology (e.g. Sade and Dow 1994, Pepper et al. 1999) where the similarities to HSNs are more evident.

HSN studies gather data mainly via surveys and questionnaires (Marsden 1990). The crucial difference with ASNs is that unlike with humans, we cannot simply question animals about who they prefer to associate with or who they interact with. Instead we must rely on observations of animal behaviour to try to ensure we build as accurate a picture as possible of the true social structure. A consequence of this is that for ASNs there is often uncertainty in the association data which leads to uncertainty in network edges.

Another difference is that for HSN studies it is possible to gather complete information on the ties linking all individuals in a closed population (e.g. all individuals in company) (Marsden 1990). With the exception of captive populations this sort of ‘complete’ information is rarely available for animals. Instead ASN studies usually sample the population, gathering information on only a fraction

of the population and a fraction of the social ties.

For all these reasons, we must be more cautious when analysing animal derived network data and not all methods used for HSNs are applicable to animals. In this chapter I will introduce the main considerations when conducting ASN analysis. I begin with the issues unique to collecting data on animals and then move on to common methods of analysis.

3.1 Data collection

3.1.1 Animal identification

The first prerequisite for recording animal behaviour is that the animals are identifiable. For large animals this may be possible using visual or photo identification using some characteristic feature. Examples of this include nose shapes for gorillas (Fossey 1983), shape of dorsal fin for sharks (Mourier et al. 2012) and neck markings for giraffes (Shorrocks and Croft 2009). Another common method for smaller or hard to identify species is to mark the animals in some way. A procedure used for *Leptothorax* ants involves marking ants' gasters with coloured droplets of paint so that each ant has a unique colour code (Sendova-Franks and Franks 1993). An equivalent method was used for the population of Trinidadian guppies studied in Chapter 5 (see Sec. 5.3 for details).

It may also be possible to attach electronic tags to the animals. Passive Integrated Transponder (PIT) tags fitted to animals can be read by detectors in order to identify the animal (Krause et al. 2011). Usually between 8–32 mm long (Smyth and Nebel 2013) they are small enough to be used on small animals and have been used on a wide range of species including great tits (*Parus major*) (Psorakis et al. 2012), Atlantic salmon (*Salmo salar*) (Roussel et al. 2000) and manatees (*Trichechus manatus latirostris*) (Wright et al. 1998).

3.1.2 Interactions vs associations

Network studies on animals fall into two categories, those based on interactions and those based on associations. Interactions are observable events such as grooming, feeding, copulating or displays of aggression whereas association is inferred through spatial proximity, nearest neighbours, shared space use or group membership. Network studies based on interactions have the advantage that observing an interaction is unambiguous and so the researcher can have confidence in the resulting network edges (Croft et al. 2011). It is not always possible however to record interactions as they could happen out of sight of the observer (Whitehead 2008b) or infrequently (Croft et al. 2011). In these cases it may be beneficial to record association data instead.

Whitehead defined association as a state where interactions (either visual, vocal or physical) are possible (Whitehead 2008b). Precisely what conditions are needed for interactions to be possible are unlikely to be known and so usually researchers make a judgement call on the spatial proximity required based on past research (Whitehead 2008b, Haddadi et al. 2011). It is also a judgement call as to whether inferring association by nearest neighbour or by group membership is appropriate for a species. The consequence of inferring association in these ways is that there is more uncertainty in the resulting network edges. Occurrences of association may have been recorded in situations where the animals were not in fact associating. They could for example have been in close proximity purely by chance as they passed by each other moving in opposite directions. The uncertainty this produces in the network edges means extra care must be taken when analysing networks built from associative data (Croft et al. (2011)).

The networks considered in this thesis are built from association data. The networks of the Trinidadian guppy studied in Chapter 5 are constructed using group membership as a proxy for association. Consideration of the best way to analyse such data lead to the work in Chapter 6 where I consider ways to improve existing tools. Association data for the New Caledonian crow used in Chapter 7 used spatial proximity as a proxy for association.

3.1.3 Sampling protocol considerations

Having decided what behaviour is to be observed, the next challenge is to find the most appropriate method of data collection. This is a far more difficult task for animal social networks than for those based on humans and it is usually impossible to collect a complete data set. Even what constitutes a complete data set is often unclear.

Collecting a complete data set may be possible when recording interactions amongst captive populations for example occurrences of grooming amongst gorillas in a zoo. In such cases the number of animals may be small enough and the rate of interaction low enough for an observer to manually record all instances of the interaction during the study period and this would constitute a complete data set. Technology may also be employed to help with this in the form of video recording all the animals so that interactions can be recorded after the event either through manual playback or with the help of software to identify the interactions (e.g. Sendova-Franks et al. 2010). Video recording would also facilitate obtaining a complete set of association data from a captive population as it would be possible to find the spatial proximity of all pairs of animals as a near continuous function of time or record all group memberships.

Recent advances in technology have enabled associations to be recorded between animals in the wild (Krause et al. 2013, Ryder et al. 2012). Associations can be gleaned from the collected data either directly or indirectly (Krause et al. 2013). Proximity loggers such as Sirtrack (Prange et al. 2006) and Encounternet (Mennill et al. 2012, Rutz et al. 2012) record associations directly using transceivers which are fitted to the animals. When two animals come within range of each other both transceivers log the event, labelling it with the identification code of the other device. This yields a list of timestamped encounters which has the potential for temporal network analysis. The data used in Chapter 7 are of this nature and were collected using Encounternet (a more detailed explanation of how it works is included there). Associations can also be inferred indirectly by using technology that maps spatio-temporal movements of animals (Krause et al. 2013). GPS logging, VHF radio-telemetry or acoustic telemetry systems record movement paths of animals via tags attached to the animals (Krause et al. 2013). Associations can be inferred by collating the movements of all animals and locating occurrences of animals being in close proximity. Systems with fixed receivers

(e.g. PIT tags) log individual visits to the receiver sites and associations are inferred from co-visits to the receiver site.

Although there are many benefits from the large and detailed data sets which these new technologies can collect, there are limitations to their use. Primarily, the technology must be appropriate to the study species. The smallest available proximity loggers weigh around 9 g and are too heavy for some bird species (Rutz et al. 2012). Typically the smaller the tag the smaller the battery life and available memory and so the behaviour of the species may become an important factor in whether enough data may be collected given the limitations of the tag (Krause et al. 2013). The habitat of the study species may also be a limiting factor. Some technologies are ideally suited to either terrestrial or aquatic species (Krause et al. 2013). Finally cost may be an issue. Many of the devices are expensive to deploy and so the number of tags used may be limited. A comprehensive review of the pros and cons of different technologies is available in Krause et al. 2013.

Without the aid of technology, it is usually impossible to obtain such a detailed data set. Animals may be out of sight of the observer for many reasons such as dense vegetation resulting in poor visibility, animals may spend a considerable amount of time in burrows or the home ranges of animals may simply be so vast that the animals are too far away to be seen (Whitehead 2008b). This means that observing all the interactions or associations during the study manually will often be impossible. Instead it is necessary to use a sampling method to gather the best data set possible.

There is a wealth of literature available on manual sampling techniques with a significant review of different methods given in Altmann (1974). Methods similar to Altmann's scan sampling are often used for ASN studies. In scan sampling, sampling sessions are held at predetermined times and the associations between as many animals as possible are recorded. Sampling sessions are often also referred to as censuses and I shall use this terminology in the remainder of this thesis. Examples where this has been used include spider monkeys (*Ateles geoffroyi*) (Ramos-Fernández et al. 2009) and Galàpagos sealions (*Zalophus wollebaeki*) (Wolf et al. 2007). This is also the method used for the Trinidadian guppy (Ch. 5) and it will be discussed in more detail in Section 4.1.

An important consideration when sampling animal populations is deciding which

animals should be included in the study. This is known as the ‘boundary specification problem’ (Laumann et al. 1983). Wild populations of animals are in general not closed systems, animals are linked socially to other animals through associations, so unless the population is completely isolated there is no well defined ‘edge’ to the population. Networks of such populations can be misleading as animals having few network ties may simply be associating with animals not included in the network. A snowballing sampling technique used for HSNs is aimed at solving this problem (Goodman 1961). This involves defining a core group of individuals known as the ‘first order zone’ (Wasserman and Fause 1994). Associations are determined between all animals in the first order zone. Animals not themselves in the first order zone but found to have direct associations with animals in the first order zone are placed in the ‘second order zone’. Animals not having a direct association to those in the first order zone are placed in the third order zone. Sampling continues until there is confidence in the network structure of the animals in the first order zone.

Although popular for HSNs, snowball sampling is not generally used for ASNs. In order to determine the social structure of the individuals in the first order zone it is necessary to include many more individuals comprising the second and possibly third order zones. The effort required to achieve this is far too costly for animal populations. Instead biologists try to choose populations which are closed or nearly closed. When this is not possible one way to decide which individuals to include in the network is to use a filter. Networks may be filtered to include only edges with an edge weight above a threshold and individuals observed a minimum number of times although little research has been done into the precise effect of removal of edges and nodes on network properties (Franks et al. 2010, Croft et al. 2008). Filtering however comes at the cost of discarding data in what in many cases may already be a small data set. The benefits of filtering must therefore be balanced against the need to keep as much data as possible for statistical analysis.

Further consideration must be given to determining the duration and number of censuses, each of which must be relevant to the research question. If the aim is to build a static ‘snapshot’ of the social structure then the total duration in which all censuses are conducted should be short relative to any long term changes in social structure such as seasonal variations or births and deaths. Too short a duration however and the full complexity of the structure may not be captured. In general,

the more censuses the better as increased numbers of observations increase the precision of the measures of association (Whitehead 2008a). However, it may not be practical to perform large numbers of censuses and so a compromise must be reached. Franks et al. (2010) gives a guide to how many censuses are required for calculated network measures to give an adequate estimate of true values.

If the research aim is to study the dynamics of a network over time the frequency of censuses is also important. The frequency must be appropriate to the time scale of the dynamics being studied. For example a study of the seasonal variation in Asian elephant networks in Uda Walawe National Park conducted censuses on two or three days per week over the course of two years (de Silva et al. 2011). In contrast when studying processes which can happen more rapidly such as spreading of information or disease then sampling needs to be performed more frequently. Haddadi et al. (2011) provides methodology for determining the minimum sampling rate required in order to capture network dynamics and tested this on Merino sheep. In order to distinguish between periods of different activities (e.g. ‘herding’ or ‘in field’) in sheep networks Haddadi et al. found that censuses needed to be less than 1 minute apart.

Finally it is worth bearing in mind that sampling is often uneven and this can introduce biases into the edge weights. In most cases, not every animal will be observed in every census and this can bias the data if the probability of observation is not random with respect to the individual (Altmann 1974, Klaich et al. 2011). This could happen in a variety of ways for example some animals could be more shy than others and actively hide from being observed. This may erroneously make them seem less sociable than others. Alternatively animals may be more or less likely to be observed when they are associating compared to when they are not (Cairns and Schwager 1987). These biases (and many more) could lead to the measured network misrepresenting the social structure of the population. One way of rectifying this to some extent is to use an association index (AI). AIs and their use in compensating for bias are the subject of Chapter 6.

3.2 Quantifying and describing an association network

Once the data have been collected the next step is to represent them as a network. The network may be binary, an edge is present between two animals if they have ever associated, or weighted, where the edge weight is representative of the association strength. The edges may also be directed, for example A is the nearest neighbour of B , or undirected. It is the general consensus that weighted networks are preferable to binary ones (Lusseau et al. 2008, Whitehead 2008b). Information is lost when using binary networks so there is no differentiation between the edges. In a population where all animals associate with all other animals a binary network would not be useful for illustrating the social structure (Lusseau et al. 2008). Whitehead (2008b) also makes the point that although an observer may be able to say with certainty that two animals have interacted, it is much harder to be sure that two animals have not interacted and thus there will be less confidence in the absence of edges than the presence of edges in binary networks. Although weighted networks are preferable there are fewer tools available for their analysis. Analysis methods are however being developed; some interesting examples can be found in Newman (2004), Barrat et al. (2004) and Opsahl et al. (2010).

Association indices (AIs) can be used to quantify the strength of association between pairs of animals and hence assign edge weights. The most obvious way of weighting an edge is to use a simple count such as the number of times animals are seen in the same group. A simple count can however is often subject to biases introduced at the data collection stage and so other AIs have been developed to improve things (Cairns and Schwager 1987, Ginsberg and Young 1992, Whitehead and Dufault 1999). Association indices are the subject of Chapter 6 where I present a comprehensive review of indices used and suggest modifications to existing indices which can be used for group based data.

After the edge weights have been determined the network can then be drawn. Nodes can be shaped or coloured to represent node attributes and edges may have varying widths to represent the association strength. This is an important step as visualisation can suggest new lines of research (see Fig. 3.1 for an example). Network and node measures as described in Section 2.2 are used to describe the

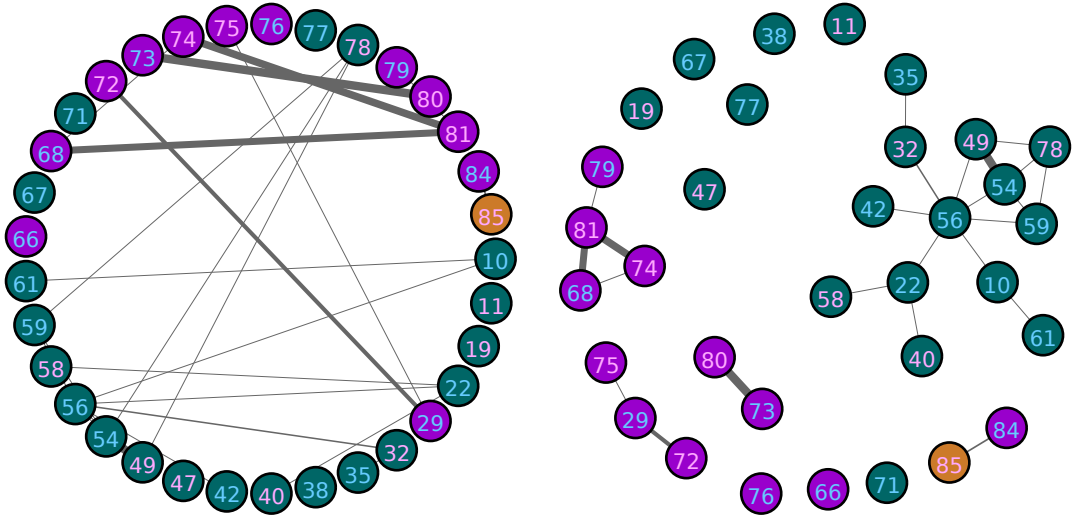


Figure 3.1: *Two visualisations of a social network of New Caledonian crows (data from Ch. 7). Nodes are coloured according to the location in which the crow was captured and node labels are coloured according to the sex of the bird (pink for female and blue for male). In a) nodes are laid out around a circle whereas in b) nodes have been laid out according to a ‘spring-embedding’ algorithm. b) shows the advantage of effective visualisation. It shows that (with the exception of crows 84 and 85) all edges are between crows from the same capture site. The layout also highlights crow 56 as having the highest degree of 7 and appears to be central to the network.*

network quantitatively. Node centrality measures are often used to describe an animal’s position within the network for example node strength (e.g. Lusseau et al. 2008) and eigenvector centrality (e.g. Gero et al. 2013). Network measures are used to characterise the overall network structure for example characteristic path length (e.g. Opsahl et al. 2010). Node and network measures are purely descriptive and in order to go beyond this and test biological hypotheses statistical analysis tools must be used.

3.3 Statistical analysis

A common aim of ASN studies is to discover which factors influence the structure and dynamics of the social network and the relative importances of the different factors (Sih et al. 2009, Whitehead 2008b). Possible factors (or explanatory

variables) include individual data (e.g. sex, age, body size), relational data (e.g. genetic relatedness, home range overlap) and environmental data (e.g. resource distribution). As pointed out in Section 2.2.1, the primary difficulty in analysing network data is that the data points are not independent (Croft et al. 2011). Simple statistical significance tests often assume data points are independent and so alternative ways of dealing with network data must be found. There is a range of statistical tools available to help with this, some used more widely than others, and all tools have their advantages and disadvantages.

Methods generally fall into two classes, those that create a model, and those that use a null model and test hypotheses. Developing a model involves finding the mix of explanatory variables which is most likely to produce the observed network. In contrast when using a null model the null hypothesis states that the network is no different than would be expected by chance and a test hypothesis states that some feature of the network cannot be explained by chance. This section presents an overview of both types of method.

3.3.1 Models for static networks

Many techniques fall under the umbrella of developing a model of the system in order to explain the social network structure. These techniques generate networks based on one or more explanatory variables with parameters controlling the influence of each variable. The models can then be fitted to the real data using a measure of ‘goodness of fit’ such as Akaike’s information criteria to determine the combination of variables which is sufficient to explain the observed network structure (e.g. Aplin et al. 2012).

One modelling technique, Exponential Random Graph Modelling (ERGM) or p^* modelling, uses stochastic modelling to obtain the probability that a network edge exists based on a set of explanatory variables (Pinter-Wollman et al. 2014, Robins et al. 2007). ERGM can be used with multiple and correlated variables, however a major drawback is that it can only be used with binary networks (Pinter-Wollman et al. 2014).

A second type of regression modelling, General Linear Models (GLMs), is often used for non-network data to assess the contribution of multiple explanatory

variables to one dependent variable. The dependent variable is expressed as a linear combination of the explanatory variables each multiplied by a parameter to be determined. These are however inappropriate for network data as they assume data points are independent (Hoff 2003). Instead it is possible to use Generalised Linear Mixed Models (GLMMs), also called Random Effects Models, which incorporate an extra random effect term into a GLM (Muccullock and Neuhaus 2013). The random effect term can be used to model different types of dependencies in the dependent variable (discussed in Sec. 2.2.1) although modelling every type of dependence is non-trivial (Hoff 2003). Advantages of GLMMs over ERGMs are that they can be used with weighted network data and explanatory variables can be continuous.

Whilst being seemingly attractive, regression models such as GLMMs and ERGMs have yet to be proved suitable for ASNs. p^* and other related models have been used for HSNs (Wasserman and Pattison 1996) but the requirement of having a binary network substantially limits their usefulness and they have yet to be applied to ASNs (Pinter-Wollman et al. 2014). GLMMs have rarely been applied to ASNs (two exceptions being Godfrey et al. (2009) and Wey and Blumstein (2012)) and more work is required to adapt them to the many types of dependencies present in network data. For ASNs in particular it may be difficult to place all the necessary constraints on the model. One such constraint, described in the next chapter, is the need to control for group size in data originating from group observations.

3.3.2 Null models and hypothesis testing

In contrast with constructing a model, an alternative is to use null hypothesis significance testing (NHST). A typical null hypothesis would be that some aspect of the network is no different than would be expected by chance. Node or network based measures are used in order to calculate some property of the network t to use as a test statistic. An ensemble of at least 1000 randomised permutations of the real network is created and t is calculated for each of the randomised networks to obtain the distribution of t under the null hypothesis. The observed value t_{obs} can then be compared to this distribution. If t_{obs} falls near the middle of the distribution then t_{obs} is a likely observation under the null hypothesis. If however t_{obs} falls near the tails of the distribution then it is far less likely under the null

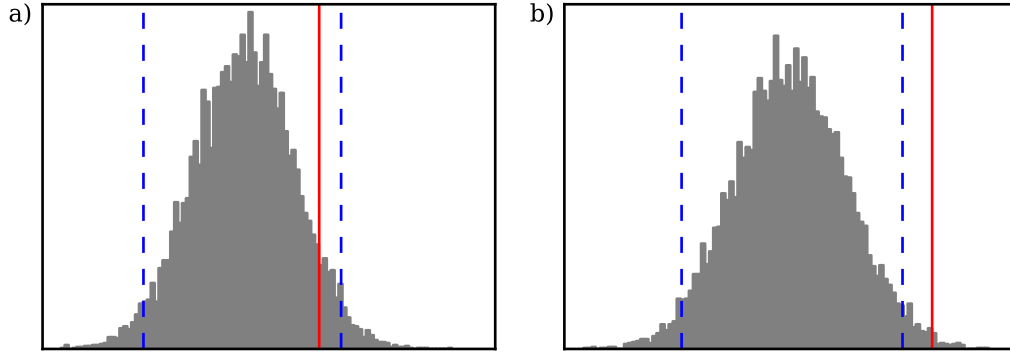


Figure 3.2: *Illustration of null hypothesis significance testing (NHST). The histograms show the distribution of an imaginary test statistic t obtained from 10,000 randomised permutations of the real data. The significance level used here is $\alpha = 5\%$ which for this two-tailed test is split between the upper and lower ends of the distribution. Blue dashed lines show the positions of the 2.5th and 97.5th percentiles of the distribution outside which t_{obs} would be considered significant. Red lines indicate the value of the observed t_{obs} . In a) t_{obs} does not lie either below the 2.5th or above the 97.5th percentiles. This means it is likely that the value t_{obs} could have arisen by chance and so the null hypothesis is not rejected. In b) t_{obs} lies above the 97.5th percentile meaning that it is very unlikely this could have happened by chance. In this case the null hypothesis is rejected.*

hypothesis that t_{obs} would be observed. A significance level α can be used to accept or reject the null hypothesis. The choice of α is arbitrary although it is usually 5% or less. If the probability of observing a value greater than or equal to t_{obs} (or less than or equal to t_{obs} for the lower tail of the distribution) is less than α then the null hypothesis is rejected (Fig. 3.2).

The procedure used to generate randomised networks must be carefully considered as the biological assumptions it is based upon must be relevant to the study system and the biological question. The simplest randomisation procedure is a node-label permutation. This is a commonly used procedure in cases where the measured network structure is assumed to be correct. A basic null hypothesis in this case is that any animal can occupy any position in the network. Extra constraints can be placed on this such as restricting the positions which females occupy in the network (Croft et al. 2011).

Methods similar to node-label permutations are used to study the dependence of the network on other relational variables. Mantel tests (Mantel 1967) calculate the correlation between matrices and effectively use a node-label permutation to test the significance of the correlation (Croft et al. 2008). The Quadratic

Assignment Procedure (QAP) similarly calculates the correlation between two matrices and then randomises the row and column order to assess significance (Dekker et al. 2007). Although rarely used for ASNs, one example is Wey and Blumstein 2010 where QAP was used to test the effect of age, sex and relatedness on a social network of yellow-bellied marmots (*Marmota flaviventris*). If there are other variables for which the association between the two matrices must be controlled, then Multiple Regression Quadratic Assignment Procedure (MRQAP) may be used (Dekker et al. 2007).

Another type of randomisation is edge randomisation. Here the edges (together with their weights) are removed from the network and reallocated to connect random pairs of nodes. The null model behind this could be something like interactions are equally likely between all pairs of animals (Croft et al. 2011). There are many reasons however why this simplest unconstrained case may not be a reasonable biological null model. Spatial and temporal constraints on the animals for example could mean some pairs of animals are more likely to meet than others (Whitehead 2008b). Such constraints could be built in to the randomisation. At the very least it would be necessary to constrain the individual node degrees, which would go some way to controlling for the variation in gregariousness of individuals (Croft et al. 2011). Edge randomisations are currently seldom used (Croft et al. 2011).

For group based association data it is possible instead to randomise the group membership data. The biological null model for the simplest, least constrained case would be that animals are equally likely to be found in any group. The various ways of performing this type of randomisation will be discussed more fully in Section 4.3.

One drawback which applies to all forms of NHST described here is that the outcome is binary, the null hypothesis is either accepted or rejected. In terms of the biology this translates to statements such as ‘the network is assorted by body size’ or ‘females have a higher degree than males’. Nakagawa and Cuthill (2007) points out that this approach lacks two important pieces of information. Firstly the effect size, in other words how much higher is the average female degree compared to males. Secondly a confidence interval assigned to this effect size telling us the precision of the estimate. NHST assigns too much meaning to the null hypothesis as the same data could also be used to reject or accept any number of

alternative null hypotheses (Nakagawa and Cuthill 2007). Nakagawa and Cuthill (2007) suggest that it would be better to search for which hypotheses are likely given the data as opposed to how likely the data are under a given hypothesis. Nakagawa and Cuthill (2007) provides a basic introduction on how to calculate effect size, focussing on d statistics (standardised mean difference) and r statistics (correlation coefficient) and their respective confidence intervals. However it is mainly aimed at independent data. For more difficult cases with dependencies they suggest using mixed-effects models such as GLMs or GLMMs but as mentioned above it is so far unclear if these have the flexibility to incorporate the constraints required for ASNs.

3.3.3 Tools for processes on networks and network dynamics

Due to the difficulty in collecting temporal network data for animals, their study is less developed than that of static animal networks. The most common type of study analyses the spread of information or disease through the network. Two types of agent based models (ABMs) are typically used to study these processes – Network Based Diffusion Analysis (NBDA) is used to study the spread of information through the network and compartmental models, borrowed from epidemiology, are used to study the spread of information or disease. I will now describe each of these in turn.

NBDA

NBDA is used to study the spread of information through a network (Franz and Nunn 2009). This information could for example be some new skill (e.g. Allen et al. 2013) or the location of a new food source (e.g. Aplin et al. 2012). NBDA’s primary aim is to determine *how* the information is spread; does each animal discover the information by chance (*asocial* learning) or do animals become informed by watching (or hearing) other animals (*social* learning). For this reason NBDA is not used to study the spread of infectious disease as this is a social process.

The forerunner to NBDA was diffusion curve analysis (DCA). DCA is an agent-based model in which it is assumed that individuals interact randomly with each other (Franz and Nunn 2009). Mathematical models of asocial and social learning can be played out on the agents and these yield different shapes of diffusion curve (number of informed individuals versus time). Both models can be fitted to experimental data and the learning is deemed to be asocial or social depending on which model gives the better fit. The main issue with this method is the assumption of random mixing of the agents. Many ASN studies have revealed structure in animals' associations and interactions and so this assumption is clearly violated.

NBDA in contrast to DCA assumes that the social learning dynamics are linked to the social network (Franz and Nunn 2009). Specifically the probability that an uninformed agent A becomes informed depends on the total strength along all edges between A and any informed agents in the network (Franz and Nunn 2009). As in DCA, in a model of asocial learning the probability that an uninformed agent becomes informed is independent of how many or which other agents are informed. Maximum-likelihood techniques are used to fit both models to observed diffusion data and the model which gives the best fit indicates the learning mechanism that is more likely to have produced the observed data (Franz and Nunn 2009).

Whilst NBDA is an extremely powerful tool to model information spread Aplin et al. (2012) suggest that it is most successful when the study population is large enough for there to be a wide variation in association strengths. Obtaining large data sets for animals is difficult and for NBDA it is necessary to obtain social network data together with time-ordered diffusion data for information spreading. Obtaining such data for wild populations can require automated data collection techniques for example using PIT tags to log the identity and time of arrival of birds at the location of a new food source (Aplin et al. 2012). Aplin et al. (2012) also caution that the associations or interactions used to build the social network must be relevant to the type of information being transferred.

Compartmental models

Used in epidemiology for modelling the spread of disease, compartmental models are so-called because they divide the individuals in a population into compartments or classes depending on their infection status. The simplest compartmental model is the Susceptible-Infected (SI) model (see for example Britton 2003). Initially all individuals except one are susceptible and one is infected. For ASNs, the process is usually played out on a static network with probabilities of infection along each edge linking an infected to a susceptible individual being proportional to the edge weight. The process was first described for ASNs in Voelkl and Noë (2008). In an SI model for a network with one component the outcome is always complete infection with the network structure determining the speed. A more complex model is the Susceptible-Infected-Recovered (SIR) model (Britton 2003). Here infected individuals may also recover with a recovery probability. The SIR model exhibits more interesting dynamics as the infected proportion of the population may both increase and decrease.

This chapter concludes the introductory part of this thesis. I have introduced network theory (Ch. 2) and the application of network analysis to animal societies (this chapter). In Part II I move on to the analysis of group-derived data which includes the first data-driven chapter on the Trinidadian guppy (*Poecilia reticulata*) (Ch. 5).

Part II

Analysis of sparse group-derived data

Chapter 4

Introduction to group-based association data

Many animals live in groups, for example colonies of ants, herds of elephants or troops of monkeys (Krause and Ruxton 2002). There is large variation in group size amongst different species from relatively small prides of lions to colonies of thousands of birds or insects, with many sizes in between. Living in groups can provide animals with many benefits (Krause and Ruxton 2002). It can reduce chances of predation in several ways. Fish moving in large shoals or birds in large flocks move in synchronised motion which confuses predators (Miller 1922), groups of elephants or bison can provide protection for group members against predators and living together with con-specifics can provide increased vigilance against predators (for example in degus (*Octodon degus*) Ebensperger and Wallem 2002). There are also costs associated with group living (Krause and Ruxton 2002). There may be increased competition when foraging for food and also increased competition for sexual partners (Hobbs et al. 1996).

It is evident that for some species such as primates, complex social interactions govern group dynamics (Sade and Dow 1994). Some primates can be relatively easy to observe and distinguishable from one another. Their groups and relationships can be stable on the timescale of observations and so observing their pairwise interactions can reveal social dominance hierarchies which govern their behaviour (Sade and Dow 1994, Pepper et al. 1999). For other species such as fish or birds, social structure may be more opaque (Whitehead 1997). There may

be many more individuals living together and they are not so easily observable or distinguishable from one another. Group compositions may be fluid and change rapidly from a large set of possibilities and without closer inspection there may appear to be no structure.

Social network analysis (SNA) provides a method with which to uncover non-random underlying structure present in group living animals. An assumption commonly made is that all members of a group are associating, a method which has been dubbed the ‘gambit of the group’ (Whitehead and Dufault 1999). Repeated observations of group memberships are made and the frequency with which each pair of animals is found in the same group is used as a basis for assigning weights to edges to differentiate strong associations from weaker ones.

As outlined in Chapter 3 a group based study using SNA proceeds in three distinct steps. First the groups are observed and memberships recorded. Then an association index is used to quantify the association strength of each dyad (pair of individuals). From these data, the network can be visualised. The third step involves testing some feature of the network usually via a randomisation test (Croft et al. 2011).

This chapter provides an overview of how network studies on group based data are carried out. Here I focus on the case of group living animals where firstly the groups have rapid fission-fusion dynamics compared to the timescale of the study and secondly observations of group membership occur at discrete time intervals. Such studies can be ideal for using the ‘gambit of the group’ to uncover social preferences. Particular attention will be given to conducting studies on the Trinidadian guppy (*Poecilia reticulata*) as the following two chapters (Ch. 5 & 6) focus on this species.

4.1 Groups and their observation

There is no single definition of what constitutes a group of animals as there is wide variation between species (Krause and Ruxton 2002). For many species spatial proximity is used and this is sometimes combined with movement in the same direction or engaging in a common activity (Krause and Ruxton 2002, Whitehead

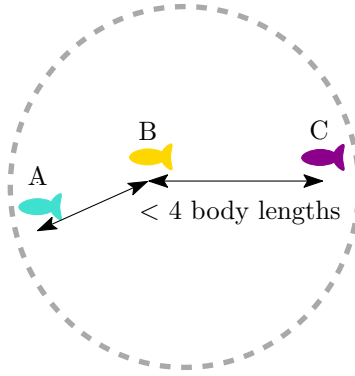


Figure 4.1: *Defining shoals of guppies using the ‘chain rule’. If B is within 4 body lengths of A and C is within 4 body lengths of B, then A, B and C are members of the same shoal (Pitcher et al. 1983).*

2008b). The amount of time which animals spend near each other may also be a factor in determining group membership. Table 4.1 lists some examples.

For the Trinidadian guppy, fish within 4 body lengths of each other are deemed to be in the same shoal (Pitcher et al. 1983). A ‘chain rule’ is applied such that if B is within 4 body lengths of A, and C is within 4 body lengths of B, then A, B and C are members of the same shoal (Pitcher et al. 1983) (Fig. 4.1).

Observing groups and identifying individuals is also done in a variety of ways. For large animals which have large home ranges, groups are often observed sequentially. Groups of African elephants are located by driving to areas where elephants are likely to be sighted (Chiyo et al. 2011). Elephants are then identified using photographs (Moss 1996). Many other large mammals are also observed in similar ways including sperm whales (Christal et al. 1998), feral cattle (Lazo 1994) and buffalo (Cross et al. 2005). Observations may be taken over any period ranging up to many years.

Sometimes it is possible to conduct a ‘census’ of the population where the group memberships of all groups are determined simultaneously. Censuses will be shown to be advantageous when it comes to the analysis of the data (Sec. 4.3). Their use is usually more practical for smaller species such as fish, insects or small mammals and is most easily accomplished in a lab where a camera can be set up to view all individuals at the same time. For the Trinidadian guppy, conducting a census is possible on wild populations through capturing individual shoals from a pool, keeping them separately until all shoals have been caught and then returning all

| Species | Proximity | Further details |
|----------------------|----------------------|---|
| Asian elephants | 500 m | Within visual range of the observer and partaking in synchronised activities or sharing resources (de Silva et al. 2011). |
| African buffalo | 1 km | (Usually a large distance (1–40 km) between groups so groups are easily distinguishable Cross et al. 2005). |
| Dolphins | 100 m | Engaged in similar behavioural activities (Parra et al. 2011). |
| Sealions | 1–2 m | (Wolf et al. 2007) |
| Sperm whales | ~3 adult bodylengths | Co-ordinated in their behaviour (Whitehead 2003). |
| Blacktip reef sharks | 15–20 m | Individuals present during the same dive and within visual range (Mourier et al. 2012). |
| Spotted hyena | 200 m | One or more individuals separated from others by ≥ 200 m (Holekamp et al. 1997). |

Table 4.1: *Definitions of groups used for different species.*

fish to the pool (see Sec. 5.3).

4.2 Quantifying association

After recording the memberships of many groups, the dataset needs to be processed in order to turn it into a network. Figure 4.2 shows the steps taken in order to do this. First, what is commonly known as a presence-absence matrix is constructed (Fig. 4.2b). This is a matrix representation of which animals were in which groups. Two different types of presence-absence matrix exist depending on whether the group data were collected using censuses or not. If group data were collected one group at a time there is one row for each individual and one column for each group observed. The matrix is then filled with ones and zeros indicating the presence or absence of each individual in each group. Alternatively, if data have been collected using censuses, then each column represents one census and the the matrix can be filled with unique group ID numbers. An entry of zero can be reserved to indicate that an individual was not found in any group in a particular census.

The presence-absence matrix can then be used to create an association matrix. The elements in an association matrix represent the association strengths between all pairs of animals in the study (Fig. 4.2c). The association strengths are calculated using an association index (AI). The simplest AI for group based data is X , the number of times two animals are found in the same group. However, in many cases this simple count is modified in order to correct for biases introduced at the data collection stage. Different possible biases and AIs designed to compensate for them will be discussed in Chapter 6. A weighted network diagram can be drawn using the association matrix to inform the edge weights (Fig. 4.2d).

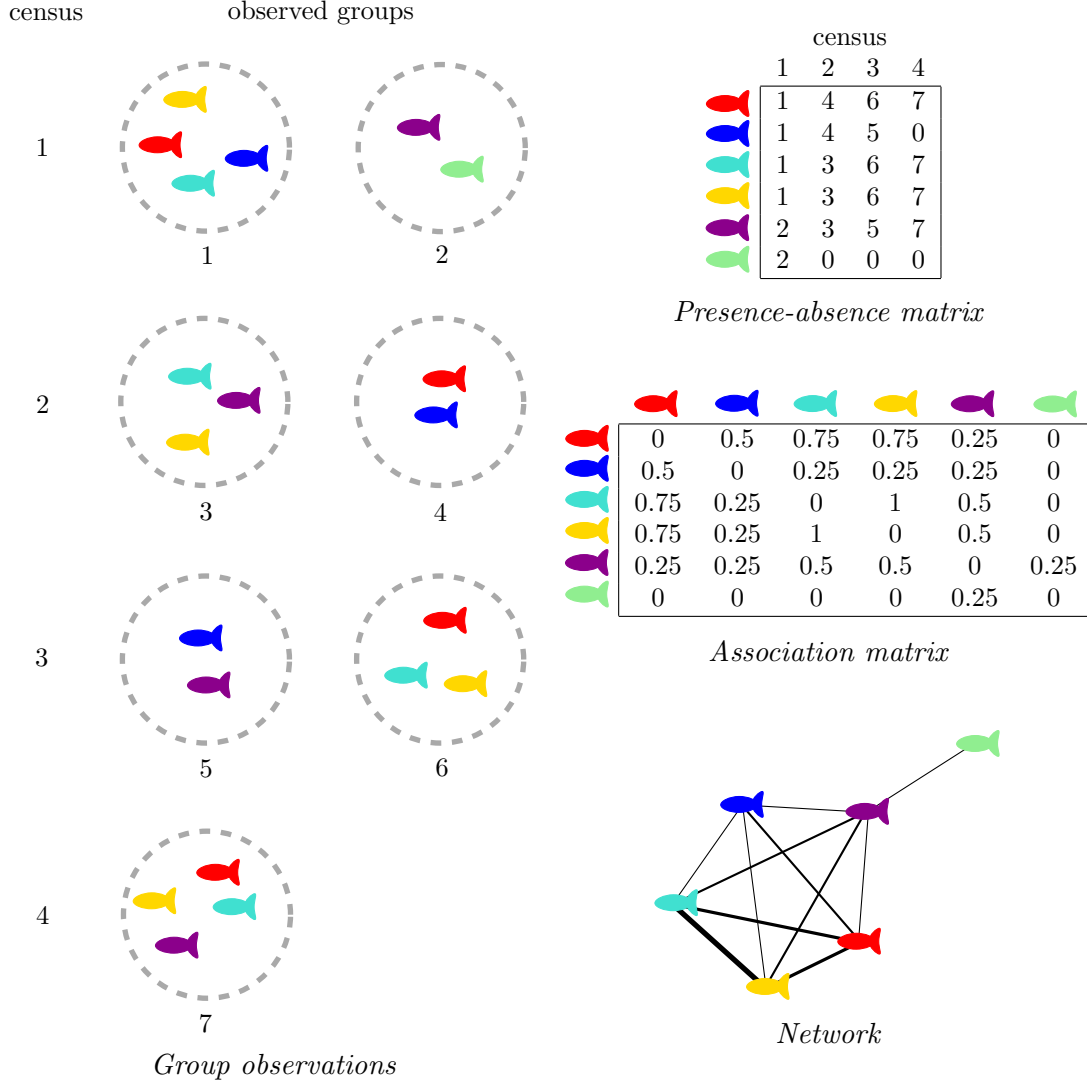


Figure 4.2: Example of how a network can be constructed from group observations of fish. a) Shows shoal compositions which were observed in four censuses. Numbers below each shoal denote the group ID number. In b) a presence-absence matrix has been filled in with the IDs of the groups in which the fish were found. An entry of zero indicates that the fish was not observed in that particular census. In c) an association index has been used to calculate the association strength between each pair of fish. In this example the association strength has been calculated as the number of times a two fish are found in the same group divided by the total number of censuses. d) Shows a network diagram constructed using the association matrix. The width of the edges represents the association strength.

4.3 Null models, hypothesis testing and randomisation

As outlined in Chapter 3, the next step is to search for rules governing the structure. The nodes of the network diagram may be shaped or coloured according to some phenotypic attribute such as age or sex, and visual inspection of the networks may suggest hypotheses such as ‘females have more network partners than males’ or ‘the network is assorted by body size’. Biologists usually have hypotheses in mind prior to constructing the network.

The basic null model for testing hypotheses on group derived data is that each animal is equally likely to be found in any of the groups. Depending on the sampling procedure, this is usually modified to refer to ‘any group within the same sampling period’. The most appropriate randomisation procedure for this null is often a group permutation (Croft et al. 2011) which will be described below.

It is important to consider whether the assumption of equal probability to be found in any group is valid. For census based studies this leads to two requirements. Firstly, within a census there is no hindrance to animals being in any group, for example spatial substructures such as home ranges or location of resources may limit movement between groups (such constraints may be implemented in the randomisation procedure by limiting which groups animals are placed in). Secondly, there must be sufficient time between censuses to allow the animals to mix fully so that the observations in each census are independent.

If a study does not use censuses then finding a randomisation which respects the potential of animals to be found in each group can be much more difficult. Group observations taken one by one over a large study area for example elephants in a national park (de Silva et al. 2011), whales in the ocean (Whitehead 1999) or deer on an island (Clutton-Brock et al. 1982) allow group memberships to change over the course of the observations. In order to randomise such data, the times and locations of the group observations must be considered together with typical travelling speeds of the animals to see which alternative group configurations were physically possible.

Using group permutation to create randomised networks is highly useful as it allows both individual observation frequencies and the distributions of group sizes in each census to be simultaneously conserved whilst allowing the network structure to change. Observation frequencies affect the measured association strengths of pairs so allowing these to vary could lead to erroneous rejection or acceptance of the null hypothesis. Similarly allowing the group size distribution to vary can have the same effect. Group size distributions are usually strongly decreasing functions of group size (Krause and Ruxton 2002) so allowing group sizes to vary freely is likely to produce group size distributions which are not found in nature.

A method of permuting group membership was proposed by Bejder et al. (1998) (adapted from Manly 1995) which has the advantage that it does not require the data to have been collected in censuses. Pairs of animals (i, j) and groups (m, n) are found where one animal is present in each group. The group membership of the pair is then swapped which has the effect of conserving observation frequency and group sizes. After many swaps are performed, the presence-absence matrix can become sufficiently different from the original and this constitutes one randomisation. Further constraints can be added to this method as required.

The data considered in chapters 5 & 6 have been collected using censuses and this facilitates the use of a different algorithm (Ward et al. 2002, Croft et al. 2004b). In this method group memberships are randomised within each census which has the advantage of conserving both group sizes and observation frequencies of each animal (Fig. 4.3). This is achieved by randomly shuffling group IDs in each column of the presence-absence matrix whilst leaving the zeros in place (Fig. 4.3b). This method has the advantage over Bejder et al. (1998) in that each randomisation is completely independent of the previous one without the need to perform many individual steps in between. Sundaresan et al. (2009) compares Bejder’s swapping method with the ‘fill’ method and concludes that both methods yield acceptable levels of false positives providing the randomisations are constrained to be within sampling time periods or censuses.

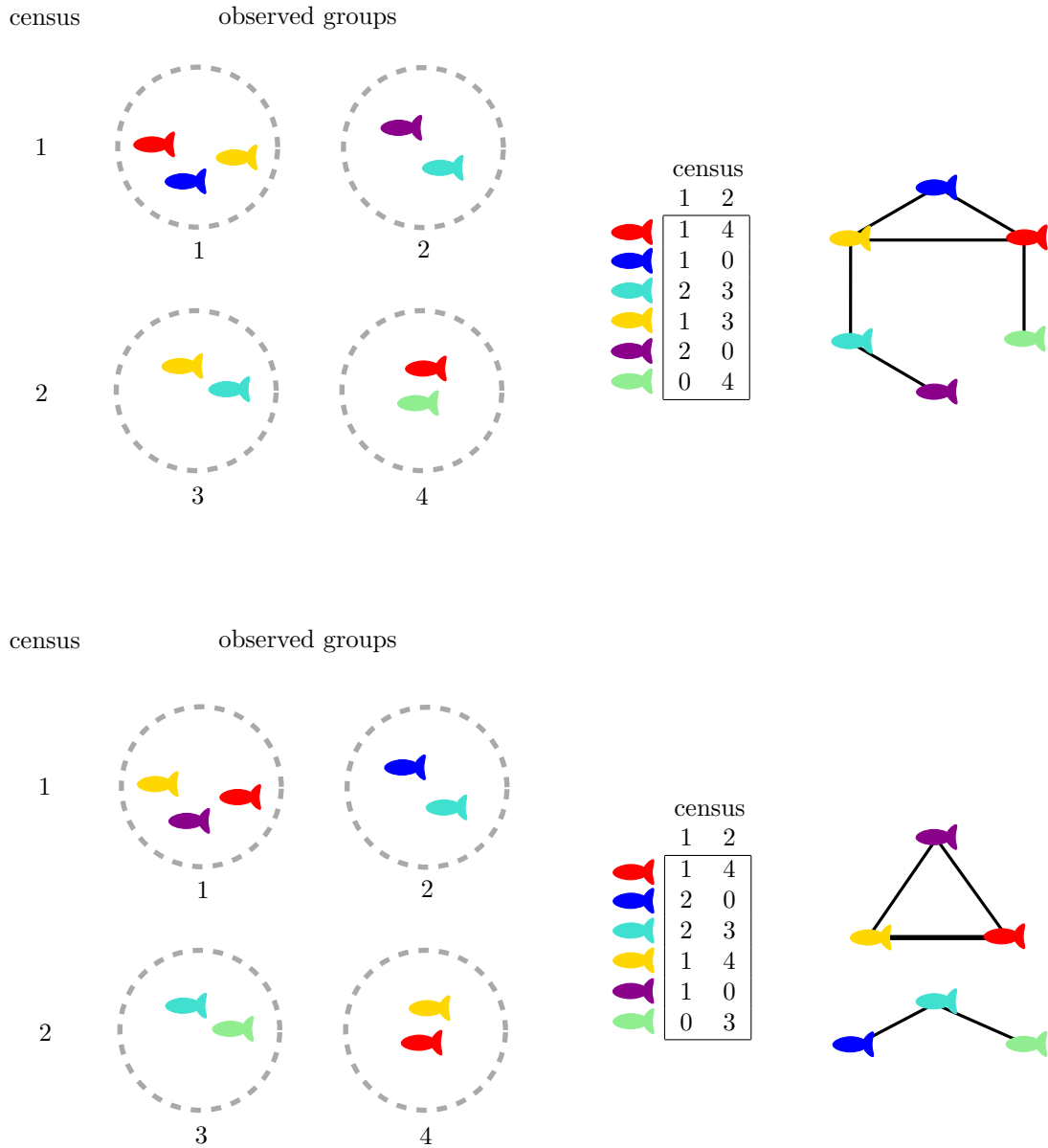


Figure 4.3: Example of within census group shuffling used by Ward et al. (2002) and Croft et al. (2004b). a) shows example group observations made during two censuses together with the corresponding presence-absence matrix and resulting network diagram. b) shows a randomised version of the observed data. The group IDs in each column of the presence-absence matrix have been shuffled leaving the zeros in place. This effectively shuffles the group memberships of all fish which were observed in each census. It preserves both the group sizes and the observation frequency of each fish.

Chapter 5

Factors influencing the social network structure of a population of wild Trinidadian guppies (*Poecilia reticulata*)

The analysis in this chapter was carried out in collaboration with Croft and co-workers and contributes to their ongoing investigations into the factors driving the social structure of wild Trinidadian guppies (*Poecilia reticulata*). The field work was carried out by Croft and co-workers and the analysis presented here, unless otherwise stated, is my own.

The work in this chapter is organised as follows. First I introduce guppies as a study system, explain why guppies are a popular study species and review previous social network studies on guppies. I then describe data collection in the current study and build some preliminary networks. The main portion of work builds on previous network analyses of wild guppies and aims to investigate the role of relatedness in structuring the social network. This section of work was published in Croft et al. (2012). There is then a further section of analysis on the same study population investigating the role of male colouring in structuring the male-male social network. This work has not yet been published.

5.1 Introduction

Guppies are small fish which are abundant in many areas of the world (Magurran 2005). They have become somewhat of a model study species because of their versatility and suitability for studying a range of areas of biology. Their small size is convenient for experiments in the lab as they can be kept in large numbers in relatively small tanks. Lab based studies are useful for investigating topics such as personality (e.g. Croft et al. 2006) and behaviour (e.g. Darden et al. 2009). In the wild they live in many diverse habitats which provides an opportunity to study the evolution of behaviours via comparative studies.

The Trinidadian guppy (Figure 5.1), the subject of this chapter, is found in a series of high predation rivers in the Northern Mountain Range of Trinidad. These rivers provide a range of differing ecologies in terms of predator densities and food sources both between rivers and along their lengths. The effects of differing ecologies on guppy behaviour may be investigated through comparative studies on multiple populations (Botham et al. 2008, Croft et al. 2009a).

The evolution and maintenance of co-operative behaviour has long interested evolutionary biologists (e.g. Darwin 1859, Hamilton 1963, Dugatkin 1997) and the Trinidadian guppy provides a system for testing some of the ideas. Co-operation between two animals is defined as an animal performing an act incurring a *cost* to itself in order to give some *benefit* to the other animal. Darwin's theory of evolution does not provide a satisfactory explanation for how co-operation has evolved and since 1960 additional mechanisms have been proposed to provide a better explanation (Axelrod and Hamilton 1981).

One mechanism via which co-operation may occur is called *mutualism* and group living is an example of this (Whitehead 2008b). As outlined in the previous chapter the group can provide benefits to all its members such as increased vigilance against predators and help with foraging. However this comes at a cost as a group is more conspicuous to predators and there can be increased competition for food (Rubenstein and Kealey 2012).

Another mechanism by which co-operation may have evolved was proposed in Hamilton (1964). Hamilton proposed a theory called *inclusive fitness* whereby

individuals behave altruistically towards others with whom they share genes such as (but not limited to) relatives. At the centre of the theory is Hamilton's rule which states that altruistic behaviour will evolve if the additional benefit to the donor is greater than the cost. This is written as

$$rB > C$$

where B is the benefit to the recipient, C is the cost to the donor and r is the genetic relatedness between the donor and recipient. rB is thus the additional benefit to the donor from the altruistic act. Benefits and costs are measured in terms of direct fitness, in other words the ability to survive and reproduce. This rule means that altruistic behaviour becomes more likely as the proportion of shared genes (r) increases.

A third theory proposed in Trivers (1971) is called *reciprocal altruism*. This states that individuals are more likely to be altruistic to others who also display altruism either towards them (direct reciprocity), or towards others (reputation reciprocity). A pre-requisite for this is repeated association between individuals so that knowledge of the other's altruistic behaviour may be acquired (Milinski 1987). This theory allows co-operation to occur between non-related individuals, a phenomenon which is perhaps harder to explain.

Co-operative behaviour is seen in Trinidadian guppies in the form of predator inspection (Pitcher et al. 1986, Dugatkin and Godin 1992). In predator inspection, performed in pairs or small groups, fish approach the predator and share the risk by taking turns to be closest to the predator. In this way they gain the benefit of knowledge about the state of the predator whilst sharing the cost of this risky undertaking. Together with their versatility for study in the wild and in the lab, this co-operative behaviour makes the Trinidadian guppy an ideal species for investigating what facilitates co-operation.

A first step to understanding who co-operates with whom could be to study who interacts with whom (Croft et al. 2006). Free-ranging Trinidadian guppies live in groups with shoals ranging in size from singletons to tens of fish. Shoals exhibit fission-fusion dynamics on a short timescale with shoals merging or splitting on average every 14 seconds (Croft et al. 2003b). At the level of the shoal assortment has been found both by sex and body length (Croft et al. 2003b). Recent studies by Croft and co-workers from 2004 onwards have taken a network approach

to analysing guppy societies and this has revealed further structure. The rapid turnover of shoal membership means some patterns may not be discernible at the level of the shoal and this is where network analysis has an advantage. As described in Chapter 4 repeated observations of shoal memberships can be used to construct a network and through network analysis, individual association preferences may become apparent and network wide patterns of assortativity may be uncovered.

Inclusive fitness is a potential explanation for co-operation between kin but an alternative explanation is needed for co-operation between non-kin. Nowak and May (1992) demonstrated that co-operation can be maintained if there is non-random social assortment, in their case modelled on a lattice. SNA is a natural way to characterise fine-scale non-random social structure; much of the work of Croft and co-workers has used SNA to try to identify the mechanisms of assortment that might enable the evolution and maintenance of co-operation among non-kin in guppies.

Assortment by relatedness amongst wild guppies is not expected for a few reasons. Guppies give birth to live offspring in large numbers and the young are immediately self-sufficient. The rapid fission and fusion of shoals then makes it unlikely that related individuals will remain together by chance. Studies searching for kin structure have so far been inconclusive. Piyapong et al. (2011) found shoals of wild juvenile guppies to be assorted by relatedness whereas studies in the lab have not found assortment by relatedness in shoals of adult guppies (Hain and Neff 2007, Russell et al. 2004). Despite the seeming improbability, it is still possible that assortment by relatedness exists in wild guppies at the network level even though fission-fusion obscures this at the level of the shoal. The current study aims to search for such assortment by relatedness at network level with the hypothesis being that the network is not assorted by relatedness.

Also presented in this chapter is an additional analysis to determine whether the body colouring of males influences male-male association patterns. Whilst related to sexual selection and not to the evolution of co-operation, this is included here as the same dataset was used and the analysis methods are common. Male guppies have areas of bright colours on their sides which has been shown to make them more attractive to females (Endler 1983, Kodric-Brown 1985). It is therefore possible that males could show preferences, either positive or negative,



Figure 5.1: *Photos showing the size of Trinidadian guppies a) male and b) female. The scales have major tick marks indicating 0.5 cm. Males have a body length of ~ 2 cm whilst females are slightly larger at ~ 3 cm. Photos courtesy of Darren Croft.*

to shoaling with other males depending on their respective colourations. For example, males could endeavour to shoal only with other males who are less brightly coloured than themselves in order to give themselves the advantage in female mate choice. If this is the case, then studying the structure of the male-male social network may confirm this behaviour. This is the first study to look at male colour patterns in the context of their social network.

5.2 Previous network studies on the Trinidadian guppy

Trinidadian guppies (males ~ 2 cm, females ~ 3 cm) (Figure 5.1) live in a series of rivers in the Northern Mountain Range of Trinidad. The rivers form a sequence of pools in which ~ 100 – 400 individuals may be found and which are connected by small riffles or waterfalls. The riffles inhibit larger predators from moving between pools whereas guppies are more able to move. On a timescale of ~ 10 days, the majority of guppies present in one pool remain, with limited instances of emigration and immigration. This means it is possible to conduct a study on a semi-closed population from one pool. Another feature of this system which makes studies easier to perform is that the water is clear, shallow and free from vegetation so that fish are easily located.

A typical study aimed at characterising the guppy social network proceeds by conducting daily censuses of a population present in one pool. During a census entire shoals are captured and the composition of each shoal recorded until there are no more marked fish remaining in the pool. After all the captured fish have

been identified, they are returned to the pool so that the procedure may be repeated the following day. The association strength calculated between two individuals A and B , corresponding to an edge weight, is based upon the number of times A and B are found in the same shoal.

This protocol is designed such that sufficient time for mixing is allowed between censuses to justify the use of a null model stating that fish are randomly grouped into shoals (see Ch. 4). There are three factors which make this null model plausible. Firstly, the pools are small enough (~ 10 m across) to enable the guppies to swim across in tens of seconds. Secondly, shoals disperse overnight and reform the next morning (Croft et al. 2003b). Thirdly and perhaps most importantly, the timescale over which group membership changes (~ 14 s (Croft et al. 2003b)) is far shorter than the periodicity of the censuses (24 h). Every 14 seconds shoals can split, merge with other shoals or exchange members with other shoals and so the timescale of 24 hours is ample time for random mixing to occur.

The first study to construct the social network of the guppy was Croft et al. (2004b). Significantly, this found evidence for repeated pairwise associations, a necessary condition for reciprocal altruism (Croft et al. 2004b). Here a census was performed on each of 7 consecutive days and a network was constructed with edges weighted by the number of times fish were found together. The resulting network of 101 individuals consisted of a ‘giant connected component’ containing all but two fish. The hypothesis that strong pairwise associations (pairs of fish which were found together 3 or more times) occurred more frequently than expected was tested against the null of shoal membership being random. Although the overall result was to reject the test hypothesis, it was found that female-female pairs were repeated more often than expected.

As described in Croft et al. (2005) the same test was performed on four separate wild guppy populations captured in different pools. When analysed separately, strong pairwise associations were found only in one population. However when combining data for all four populations it was again found that overall strong pairwise associations occurred more frequently than would be expected by chance. This study also found the network to be assorted by a range of factors. Firstly, as at shoal level, the network was assorted by body length. This was determined by finding a positive correlation between an individual’s body length and the mean body length of its network neighbours. The network was also found to exhibit

positive degree correlation (individuals are connected to others with a similar degree) although degree was also positively correlated with recapture frequency and the mean shoal size that fish were found in. The network was also assorted by mean shoal size.

Phenotypic assortment of the network was also studied in Croft et al. (2009b). Here wild female guppies were tested in the laboratory for boldness and given a score relating to their position on the bold-shy axis. Boldness was assayed using two behavioural phenotypes – the tendency to inspect predators, and the mean shoal size that fish were found in. The social network of the fish was also measured and it was found to be positively assorted by boldness score.

Croft et al. (2006) built on previous findings of stable associations in guppies and tested the propensity of guppies to engage in the co-operative behaviour of predator inspection together with fish to whom they were strongly connected in the social network. For this study wild guppies were captured and held in an arena under natural conditions. The social network of females was determined by observations of shoals. A predator was then introduced inside a transparent cylinder and occurrences of predator inspection were recorded. A positive correlation was found between the association strength of pairs and their tendency to engage together in predator inspection. Croft et al. (2006) presents evidence that ‘who co-operates with whom’ may be linked to the social structure and so understanding what drives the social structure may lead to an understanding of co-operation.

5.3 Data collection

The field work for this study was carried out in May 2009. Guppies were collected from a 40 m section of the Quare River (10°40'N, 61°12'W) in the Northern Mountain Range of Trinidad. Guppies were captured using a 2 m seine (Croft et al. 2004b) and transported in 2 L storage bags to the laboratory. Every attempt was made to capture all the fish in the pool at this time. Guppies were injected in three out of four predefined positions in the dorsal area with visible implant elastomer (VIE) (see Figure 5.2) (Croft et al. 2003a), a coloured dye, so that individual guppies could be identified. It has been shown that these



Figure 5.2: *Visible implant elastomer (VIE) was injected into three out of four positions in the dorsal area so that guppies could be identified. Each guppy was then assigned a four letter code according to the colours injected e.g. GBNY for Green, Black, No colour, Yellow. Photo courtesy of Darren Croft.*

coloured markings do not influence guppy behaviour (Croft et al. 2004b). The sex, weight and body lengths of the guppies were recorded and male guppies were photographed for colour analysis. Fin clippings were taken for molecular analysis to determine the relatedness of individuals (further details of this process are given in Croft et al. 2012). The guppies were held in aquaria for 48 hours before being released back into the centre of the pool of capture.

24 hours after release, re-sampling began and was conducted between the hours of 10:00–14:00 on 12 consecutive days. Individual shoals were captured using a 2m seine and held in a 2L container. Since the aim of the study was to analyse the social network of the guppies via their associations, guppies which were not members of a shoal (singletons) were not captured. Each shoal was photographed and then held in a 2L storage bag. When all shoals had been removed from the pool in this way, all captured fish were released back into the pool at the place of capture. The identity of guppies in each shoal was later determined from the photographs.

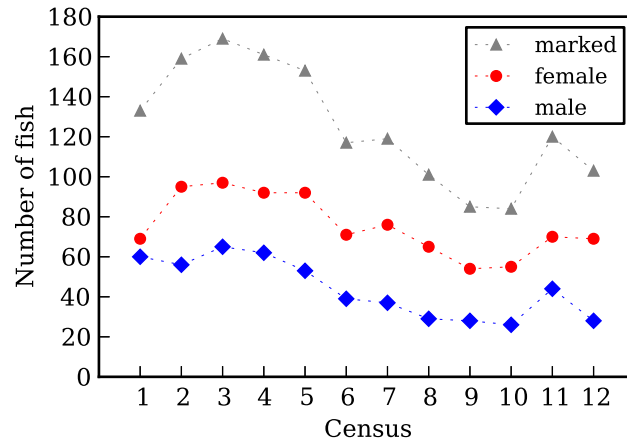


Figure 5.3: Numbers of marked fish caught in each census broken down by sex. Lines have been added to help guide the eye. The total number of marked fish caught per day decreased by approximately a third between the first and last three days of the study. When broken down by sex the number of marked males caught per day decreased by 46 % compared with just 26 % for females.

5.4 Preliminary analysis

A total of 290 fish were marked and phenotyped (157 males, 120 females, 13 sex unknown). In each census a mix of marked and unmarked fish were caught due to emigration of marked fish from the study pool and immigration of unmarked fish from other parts of the river. The total number of marked fish caught in each census decreased from an average of 151 over days 1–3 to 102 over days 10–12 (Figure 5.3). This change mainly consisted of males leaving the study pool as the average number of marked males caught per day decreased by 46 % between the first and final 3 days compared with 26 % for females. This is consistent with Croft et al. (2003a) which found emigration rates during an 8 day study to be higher for males than for females (27.3 % and 6.9 % respectively).

A total of 389 shoals were captured during the study averaging 32 per census. The distribution of shoal sizes (shown in Figure 5.4) has a mean of 8.4 fish and a modal shoal size of 4 fish. The distribution of shoal sizes is not entirely representative of the true shoal size distribution in the pool as singletons were not recorded. However the recorded distribution is a strongly decreasing function of shoal size similar to findings in Croft et al. (2003b).

When using the gambit of the group to construct a network it is necessary for

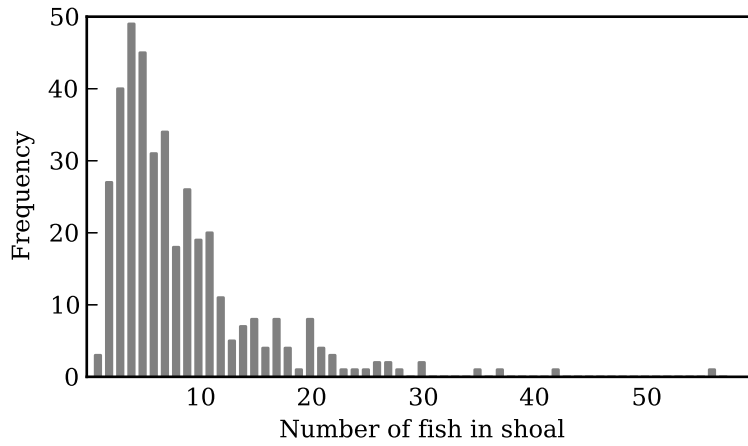


Figure 5.4: *Distribution of shoal sizes throughout the study. Shoal sizes include marked and unmarked fish. In agreement with Croft et al. (2003b), the distribution is a strongly decreasing function of shoal size.*

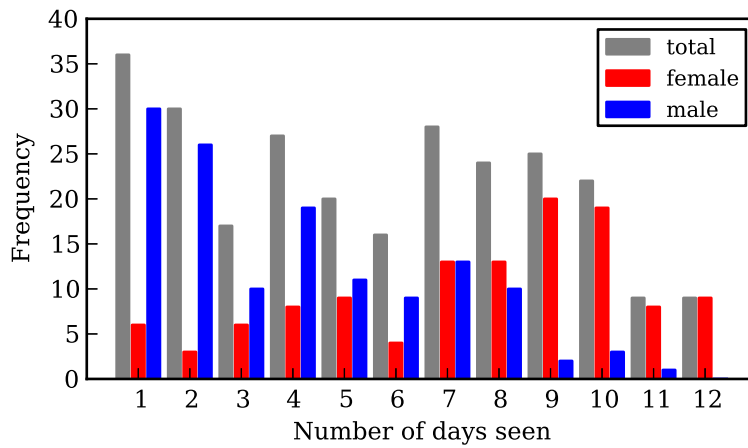


Figure 5.5: *Recapture frequency of marked fish on the 12 census days. On average females were recaptured more times than males.*

animals to be seen multiple times (see Ch. 4). Figure 5.5 shows the distribution of the number of times guppies were recaptured. Of the 290 marked fish, 264 were recaptured at least once in shoals on the 12 census days. The number of times fish were recaptured ranged from 1 to 12 times with a mean of 5.7. Females were recaptured more than often males with their means at 7.5 and 3.9 respectively.

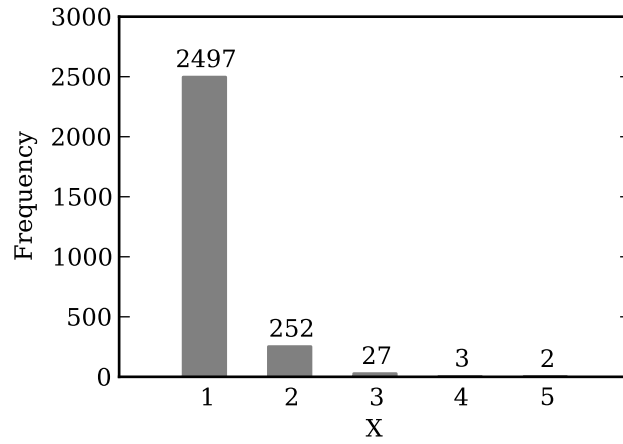
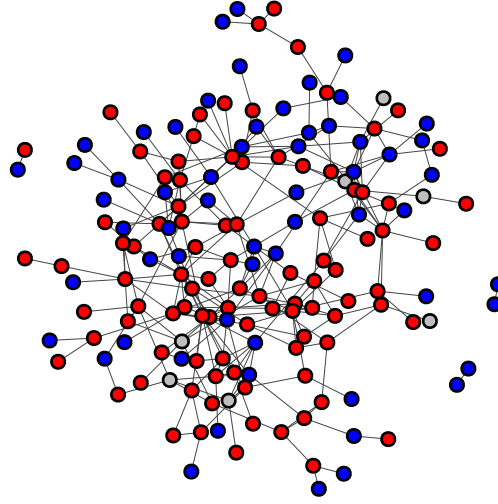


Figure 5.6: *Distribution of X for all fish which were recaptured in more than one census. 284 pairs of fish were seen together more than once*

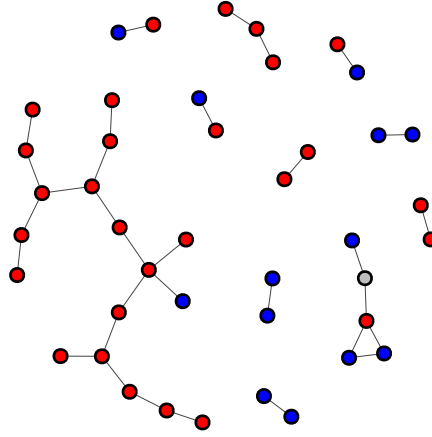
5.5 Constructing a social network

Evidence for social preferences is accumulated through repeated observations. The smaller the number of observations of an animal, the less confidence there is that its social ties have been correctly identified (Croft et al. 2008). Many studies therefore choose to filter the animals included in network analyses to those observed over a threshold number of times (e.g. Lazo 1994, Chiyo et al. 2011, Mourier et al. 2012). In this study fish which were recaptured only once were excluded from the network analyses and networks were constructed using the remaining 231 fish.

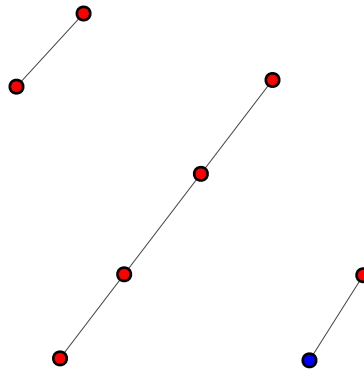
For every pair of fish A and B , the number of times A was found in a shoal with B (X) was recorded in an association matrix (Sec. 4.2). The resulting network is sparse containing 2781 edges, an edge density of 5.2%. Most pairs were only seen together once, however 284 pairs were seen together 2 or more times (Fig. 5.6). These repeated associations could be evidence of social preference and this will be tested in the following section. Figure 5.7 shows three network diagrams of these data. The dataset has been filtered to three different filter levels ($X \geq 2$, $X \geq 3$ and $X \geq 4$) to show the existing associations at different strengths.



$$X \geq 2$$



$$X \geq 3$$



$$X \geq 4$$

Figure 5.7: *Guppy network at different filter levels a) $X \geq 2$, b) $X \geq 3$ and c) $X \geq 4$. Nodes are coloured red, blue and grey to represent females, males and sex unknown respectively.*

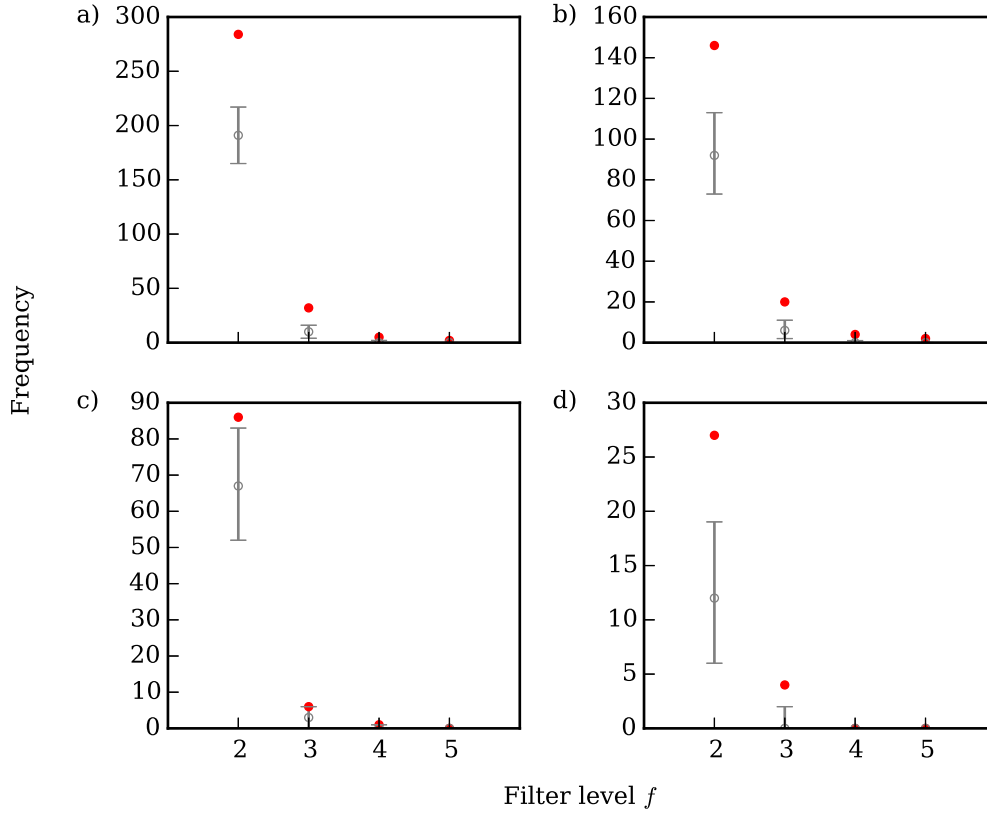


Figure 5.8: Number of network edges where edge strength $X \geq f$ for a) all pairs, b) female-female (FF) pairs, c) male-female (MF) pairs and d) male-male (MM) pairs. Observed values are marked with red circles. The distribution obtained from the null model is shown in grey with an open circle representing the median value and error bars indicating the 2.5–97.5th percentile range.

5.6 Stability of associations

As previously mentioned (Sec. 5.2), the presence of repeated pairwise associations is a prerequisite for co-operative behaviour (Croft et al. 2004b). Significant occurrence of pairwise associations in wild guppies has been found previously for female-female (FF) pairs but not for (MM) pairs (Croft et al. 2004b). The analysis here is therefore split into testing all, FF, MM and male-female (MF) pairs separately. To test if repeated pairwise associations occurred more frequently than expected, the observed frequencies were compared to the distribution given by the null model using the randomisation procedure described in detail in Section 4.3.

Shoal memberships were randomised 1,000 times preserving the presence or ab-

sence of each fish in each census. For each randomised configuration the frequency distribution of X was calculated. For a range of filter strengths ($f = 2, 3, 4$) the number of edges having $X \geq f$ in the observed network was compared to the distribution of this count from the randomised configurations. Figure 5.8 shows this comparison for a) all pairs, b) FF pairs, c) MF pairs and d) MM pairs. Comparing the observed counts with those from the randomisation showed significantly higher counts than expected for all pairs at all filter strengths ($P < 0.001$) (Fig. 5.8a). Breaking the results down by sex revealed that there were more persistent FF than expected at all filter strengths ($P < 0.001$) (Fig. 5.8b). For MM pairs, the count was only more than expected for $X \geq 2$ and $X \geq 3$ ($P < 0.001$) (Fig. 5.8d). For MF pairs, the count was only significant at $X \geq 2$ ($P < 0.05$) (Fig. 5.8c).

Having found evidence for stable relationships between FF pairs at all filter strengths and between MM and MF pairs at low filter strengths, the rest of this chapter focusses on finding features which can help explain this structure.

5.7 The role of relatedness

Pairwise relatedness values (r) are measured on a scale from 0 to 1 where 1 means the pair share 100 % of their genes and 0 means they share none. Siblings share on average 50 % ($r = 0.5$) of their genes and half-siblings 25 % ($r = 0.25$). The relatedness values between all pairs of genotyped fish ($n = 171$) ranged from 0 to 0.621 with a mean of 0.036. Most pairs were only distantly related to each other (55 % were unrelated at the resolution of the analysis and 80 % had $r \leq 0.1$) (Fig. 5.9) and most individuals had no first-degree relatives amongst the genotyped fish (Croft et al. 2012). Seven pairs were identified as full siblings (possibly parent-offspring pairs) and 352 half-sibling pairs were found (Croft et al. 2012).

5.7.1 Assortment by relatedness at shoal level

If guppies preferentially associate with kin then these preferences may be revealed by analysing the compositions of shoals. The mean relatedness within a shoal can be calculated by averaging pairwise relatedness values for all pairs of fish

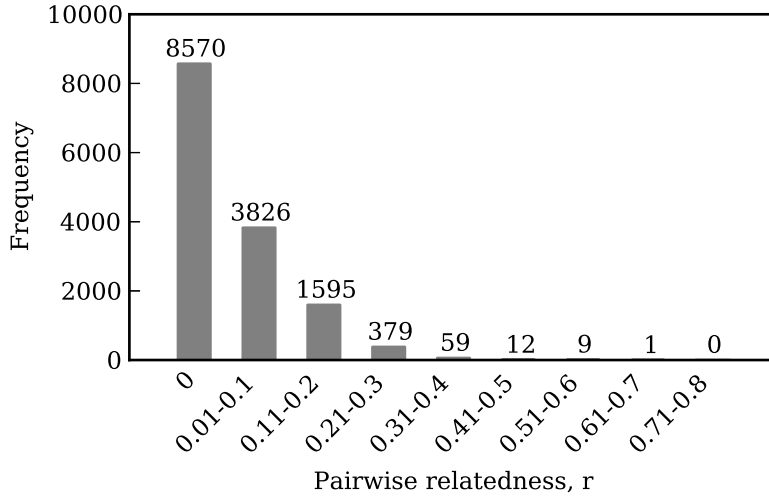


Figure 5.9: *Distribution of pairwise relatedness values between all genotyped fish ($n = 171$).*

in the shoal. If shoals are assorted by relatedness then the mean within shoal relatedness values would be higher than expected by chance.

Assortment at shoal level is tested using the group randomisation method (Sec. 4.3). To avoid pseudo-replication, shoal membership data from each census were taken separately and a test statistic and randomisation distribution are calculated for each census. Whilst pseudo-replication in the test data would not affect the outcome of a hypothesis test as the same pseudo-replication would also be present in the randomised datasets it could be informative to see the results from each census separately. The test statistic t for census c is calculated as the mean within shoal pairwise relatedness averaged over all shoals in census c . The group membership is then shuffled amongst all shoals in census c and t recalculated to give a distribution for t .

The results from the randomisation test are shown in Figure 5.10. The observed test statistics are shown by red circles and the distribution from the randomisation is indicated by a grey circle at the median value with error bars extending between the 2.5–97.5 th percentiles. There is no trend for the observed mean within shoal relatedness to be higher than the median value of t expected by chance as it is above the median in fewer than half of the censuses. The observed t was only outside the 95 % confidence interval in census 12 where t was at the 98 th percentile of the distribution. Using a 95 % confidence interval one would expect

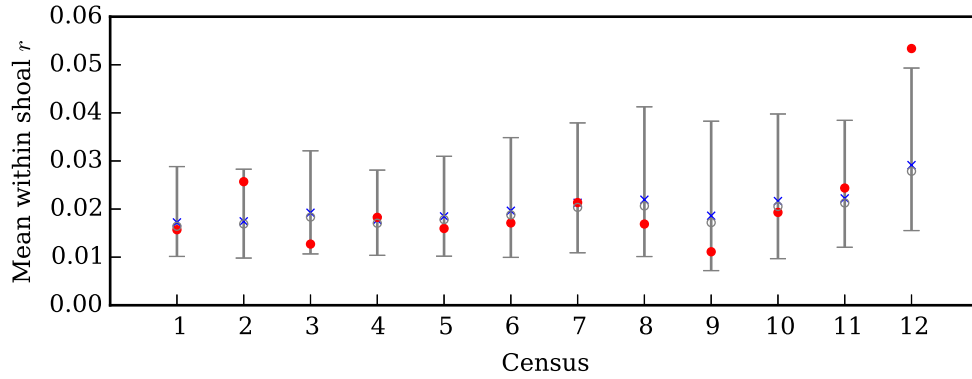


Figure 5.10: *Randomisation test results searching for assortment by relatedness at the level of the shoal. Red circles show the mean within shoal relatedness r across all shoals in one census. Grey circles show the median within shoal relatedness obtained from 1,000 randomisations of shoal membership. Error bars extend between the 2.5–97.5th percentiles. Blue crosses show the mean relatedness between all fish caught in each census.*

to erroneously reject the null hypothesis 1 time in 20 and with 12 censuses the null hypothesis is here rejected 1 time out of 12. However the observed t in most censuses is close to the median expected value and is below the median in 7 censuses. In addition the observed t is below the average relatedness of all fish caught in each census (blue crosses in Fig. 5.10) in 7 censuses. Therefore combining the evidence from all censuses I conclude that shoals are not assorted by relatedness.

5.7.2 Assortment by relatedness at network level

In this section I investigate whether guppies preferentially associate with individuals with whom they are more closely related. In network language, this equates to a positive correlation between edge strength and pairwise relatedness so that pairs of guppies which are found together many times have high relatedness values and vice versa.

Both edge strength and relatedness can be represented in matrices and the core purpose of this investigation is to search for positive correlation between them. One method of searching for correlation between two matrices is to use a Mantel test (Mantel 1967). This method calculates a correlation score Z by summing the element-wise product of the matrices. The significance of Z is then tested against

a distribution of Z produced by randomising the ordering of rows and columns of one of the matrices and recomputing Z . This randomisation procedure is equivalent to the node-label permutation described in Section 3.3.2. However as described in Section 4.3 in the case of group based data it is more appropriate to randomise by shuffling group membership.

Another consideration is the sparsity of the network. When including only genotyped fish, only 182 network edges had a weight of $X \geq 2$ with 20, 3 and 1 edges having weights of $X = 3, 4$ & 5 respectively. Since the majority of repeated associations were repeated either 2 or 3 times, there is not enough variation in X to attempt to correlate it with r . To circumvent this problem a simpler alternative method was used. First the network was filtered to an edge strength of $X \geq 2$ in order to include only repeated associations whilst still retaining edges at all relatedness strengths. Then the relatedness values were subdivided into bands ($r = 0$, $0 < r \leq 0.088$, $0.088 < r \leq 0.176$, $0.176 < r \leq 0.354$ and $r > 0.354$). Integer powers of 0.5 represent full siblings, half siblings etc. and to maximise the chances of full siblings and half siblings etc. being placed in different bands, band boundaries were chosen to be midway between these values on a logarithmic scale (i.e. $0.5^{1.5}$, $0.5^{2.5}$, $0.5^{3.5}$ etc.). The numbers of edges present in each relatedness band was then compared to the number expected from the null model of random shoal memberships. The distribution given by the null model was calculated using the same random shoal assignment procedure used for the stability of associations analysis in Section 5.6 and described in Section 4.3, randomising 1,000 times. The analysis was also broken down by sex to explore any patterns in the FF, MM and MF networks separately.

Figure 5.11 shows the results of the randomisation test. The network contained more edges than expected in the lowest relatedness bands ($r = 0$ and $0 < r \leq 0.088$) and for strongly related individuals ($r > 0.354$) (Fig. 5.11a). When broken down by sex, the network contained more edges than expected for unrelated FF and MM pairs and also for FF pairs with low relatedness ($0 < r \leq 0.088$) (Fig. 5.11b & d).

One indication of a preference for association with kin is an increase in the number of edges, compared to the expected number, as the relatedness increases. This was investigated by calculating the observed number of edges divided by the median expected number for each relatedness band and comparing the results

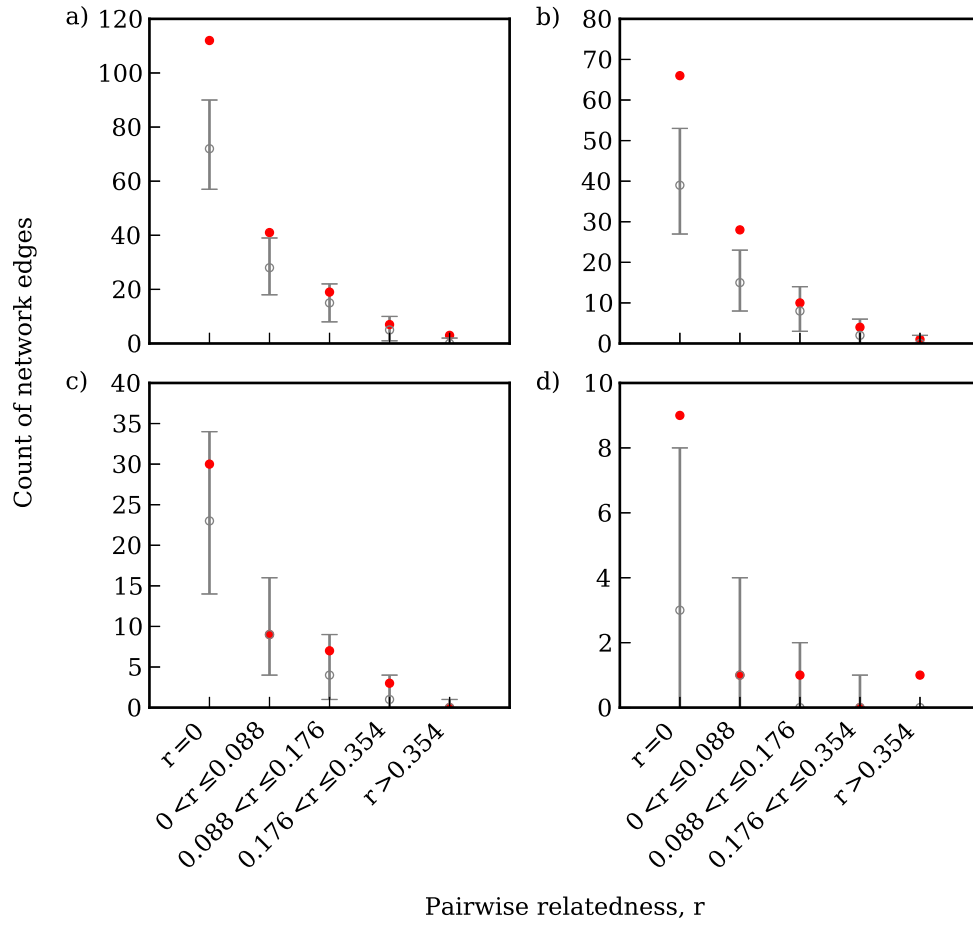


Figure 5.11: Frequency of network edges (filtered to an edge strength of $X \geq 2$) at different strengths of relatedness for a) all pairs, b) female-female (FF) pairs, c) male-female (MF) pairs and d) male-male (MM) pairs. Observed values are marked with filled red circles. The distribution from the null model is shown in grey with an open circle at the median value and error bars representing the 2.5–97.5th percentile range.

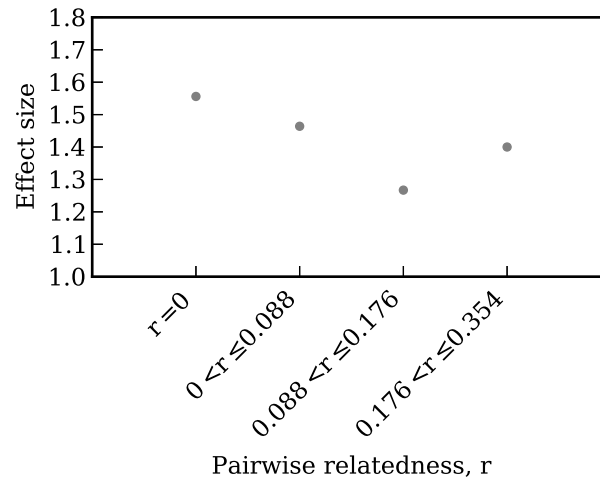


Figure 5.12: Effect size for each relatedness band. Effect size is calculated as the observed number of edges divided by the median expected value.

to see if there was a positive trend. For this analysis the maximum relatedness included was $r = 0.354$ as there were just 3 edges with a relatedness higher than this. The results for this did not show any evidence of a positive trend (Fig. 5.12).

5.7.3 Discussion

Co-operative behaviour has been observed in Trinidadian guppies when they observe predators in pairs or small groups (Pitcher et al. 1986, Dugatkin and Godin 1992). During predator inspection guppies approach predators in order to gain information on how likely the predator is to attack. Guppies share the risk of doing this by taking turns to be closest to the predator. The mechanisms facilitating the evolution and maintenance of co-operation have caused much debate among behavioural ecologists (Axelrod and Hamilton 1981). One theory called inclusive fitness, proposed in Hamilton (1964), states that individuals may behave altruistically towards others with whom they share genes. This study set out to investigate whether inclusive fitness could be a mechanism enabling co-operation in Trinidadian guppies.

In this study persistent pairwise associations were found between pairs of female guppies at all filter strengths. This is consistent with the results of Croft et al. (2004b) where persistent pairwise associations between females were also found. Male guppies gain a reproductive advantage from moving between shoals (Kelley et al. 1999) and so it was not expected to find stable relationships between MM or MF pairs. However in contrast to Croft et al. (2004b), persistent pairwise associations were also found for MM and MF pairs although only at low filter strengths. In the lab it has been shown that males can have a propensity to associate with familiar males rather than unfamiliar ones (Croft et al. 2004a). It may be that the difference in the findings of the current study and Croft et al. (2004b) could be due to differences in ecological factors affecting the study populations, for example differences in predation risk (Croft et al. 2012).

The results here confirmed the expectation of a low overall population relatedness (mean $r = 0.036$). This was anticipated as guppies are viviparous, giving birth to live young which are immediately self-sufficient. This absence of parental care means there is no reason for guppies to actively remain with kin. The rapid

fission-fusion society together with opportunity for moving between pools means that guppy populations have ample opportunity for mixing and so it is reasonable for the average level of relatedness for guppies in a single pool to be low.

Assortment by relatedness was searched for both at the level of the shoal and at network level. The results showed no evidence for assortment by relatedness at either level. This is in accordance with previous laboratory work where adult guppy shoals were not found to be assorted by relatedness (Hain and Neff 2007, Russell et al. 2004). One study did find relatedness at shoal level for wild guppies but only amongst juveniles (Piyapong et al. 2011).

Whilst it is important to remember that the evidence is based on a single population and future work on multiple populations would be required to verify the findings, the current study suggests that pairwise associations in Trinidadian guppies are not driven by kin. This means that the co-operative behaviour observed in guppies cannot be explained by Hamilton's theory of inclusive fitness, suggesting something more interesting must be at play. In the absence of kin assortment Fletcher and Doebeli (2009) showed that co-operation can evolve through assortment between co-operators and Nowak and May (1992) demonstrated that the presence of social structure can enable the maintenance of co-operation. Croft et al. (2009b) found evidence suggesting that the propensity of guppies to co-operate may structure their social network and so this could be a mechanism contributing to the maintenance of co-operation.

5.8 The role of colour in male-male associations

Male guppies are more colourful than females (Fig. 5.1) having areas of bright colours on their sides (Grether 2000). Colours and patterns are diverse and can include black, white, red-orange, yellow, green and iridescent areas, spots and lines (Houde 1997). The guppy breeding system is a female-based polygyny meaning that males compete amongst themselves for access to females (Kodric-Brown 1985) and it has been shown that females discriminate amongst males based on their colour (Kodric-Brown 1985). Male colouring, in particular the density of carotenoid pigmentation responsible for reds and oranges, has been shown to be positively correlated with swimming performance which is a measure

of fitness (Nicoletto 1991). Whilst sexual selection favours colour in males, colour patterns different from the background habitat increase the risk of predation and so the levels of male colouration are a balance between these opposing pressures (Endler 1983).

The fact that colour influences female mate choice could mean that colour plays a role in male-male associations. In order to make themselves appear more attractive, it is possible that males could seek to associate with males less colourful than themselves. This could be evident in shoal assortment by colour or by assortment at the network level. This is the first study which has considered colour in the context of social networks.

The study population for this section is the same as the previous section so no new shoaling data were collected. Photographs of captured male guppies were analysed by Safi Darden in order to collect data quantifying their colouring. Three variables were measured in order to characterise this – surface area (SA), total coloured area (TC) and the area covered by red, orange or yellow (ROY). Percentage coloured area (PC) was also calculated as $100 \times TC/SA$. Colour data were obtained for 76 males. 5 of these were only recaptured once and so as in the relatedness analysis in Section 5.5, these were removed from the shoal data leaving 71 males on which to carry out analyses. The distributions of the four colour variables are shown in Figure 5.13.

5.8.1 Assortment by colour at shoal level

If male guppies preferentially shoal with other males which have similar or dissimilar amounts of colour, then these preferences may be uncovered by analysing the shoal compositions. Shoal assortment by a phenotypic attribute such as colouration may be searched for by using the shoal memberships from one census. Using data from just one census avoids pseudo-replication of data points.

For a particular colour attribute c , the procedure for searching for assortment by c at the level of the shoal is as follows. For each shoal in one census, calculate the coefficient of variation (CV) of c for all the males in each shoal for which there is colour data. If there are k shoals in a census, then the test statistic (t) is the

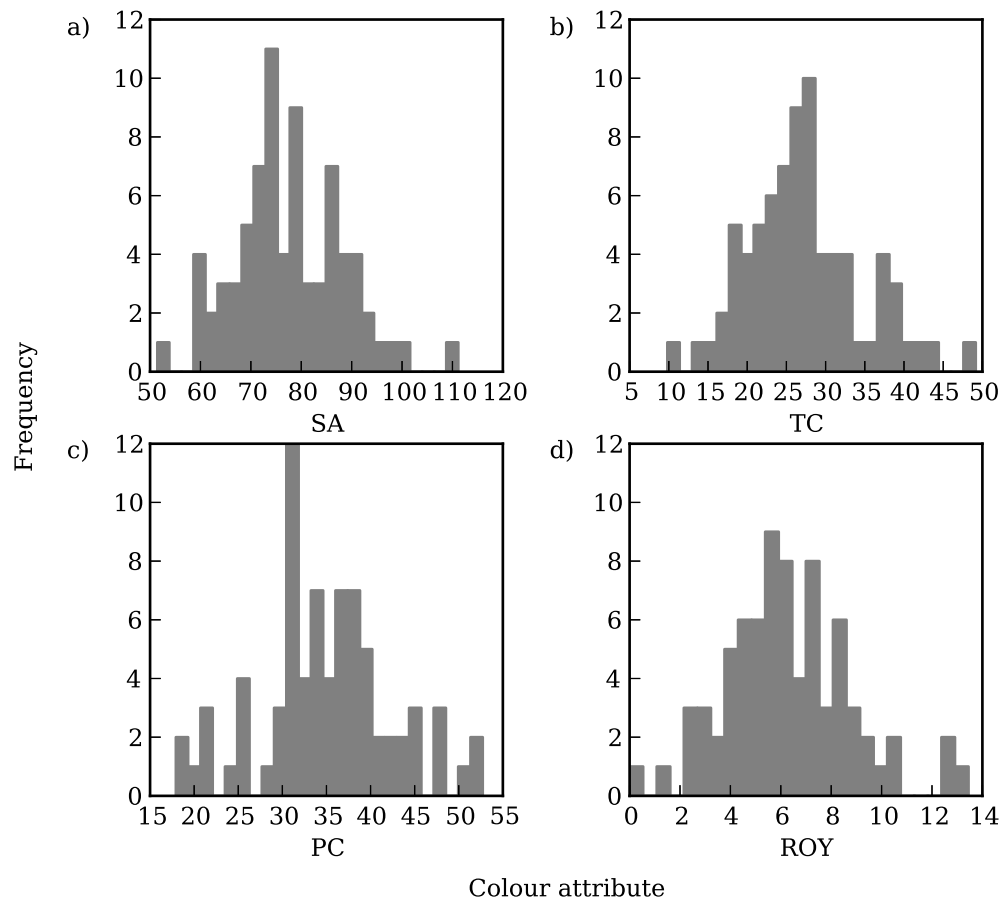


Figure 5.13: Distributions of the four colour variables for the 71 males with colour data. a) SA, b) TC, c) PC and d) ROY.

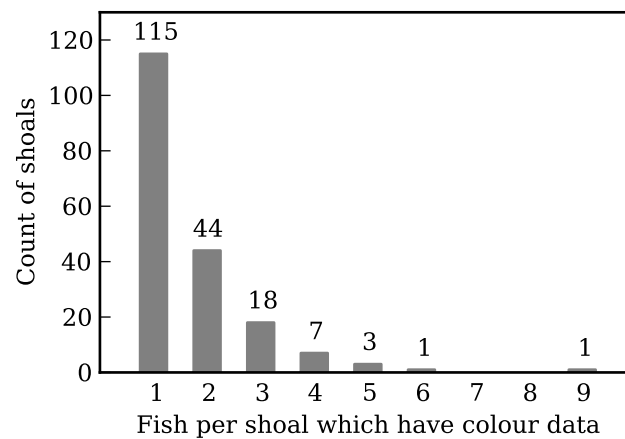


Figure 5.14: Numbers of males per shoal for which there is colour data (all censuses combined).

mean of all the shoals' CVs

$$t = \frac{1}{k} \sum_{i=1}^k \frac{\sigma_i}{\mu_i} \quad (5.1)$$

where σ_i and μ_i are the standard deviation and mean of c for the males in the i th shoal respectively (CV is sometimes multiplied by 100 to show the figure as a percentage but here this was not done). If males prefer to shoal with other males of similar colouration (i.e. brightly coloured males shoal with other brightly coloured males and dull males shoal with dull males) then the CV of c in a shoal would be smaller than would be expected by chance.

The significance of t is then tested in the same way used to search for assortment by relatedness at shoal level (Sec. 5.7.1). Males with colour data are removed from the shoals in one census and then reallocated at random preserving the sizes of the shoals. t is calculated for this random assignment of shoal memberships and the procedure is repeated 10,000 times to produce a distribution of t . The value of t from the observed data is then compared to the distribution of t from the randomised shoal data to see if t is greater than or smaller than would be expected by chance.

Shoals from each census were tested for assortment by each of the four colour variables and the results are shown in Figure 5.15. Here the observed test statistic is shown as red circles and the distribution obtained by randomisation is shown in grey as the median value, with error bars ranging from the 2.5–97.5th percentile values. The observed test statistic is never outside the range of the 2.5–97.5th percentiles and so we conclude that the shoals are not assorted by any of the colour attributes. There is also no consistency for the observed test statistic to be higher or lower than the median value of the randomisation distribution which further confirms the lack of assortment.

5.8.2 Assortment by colour at network level

As was the case with the relatedness analysis, not finding assortment at the level of the shoal does not rule out the possibility of assortment at network level. To construct a network we combine data from all the censuses and as before look at the number of times each pair of fish is found in the same shoal. For these analyses I look only at the network of MM associations for the 71 males for which

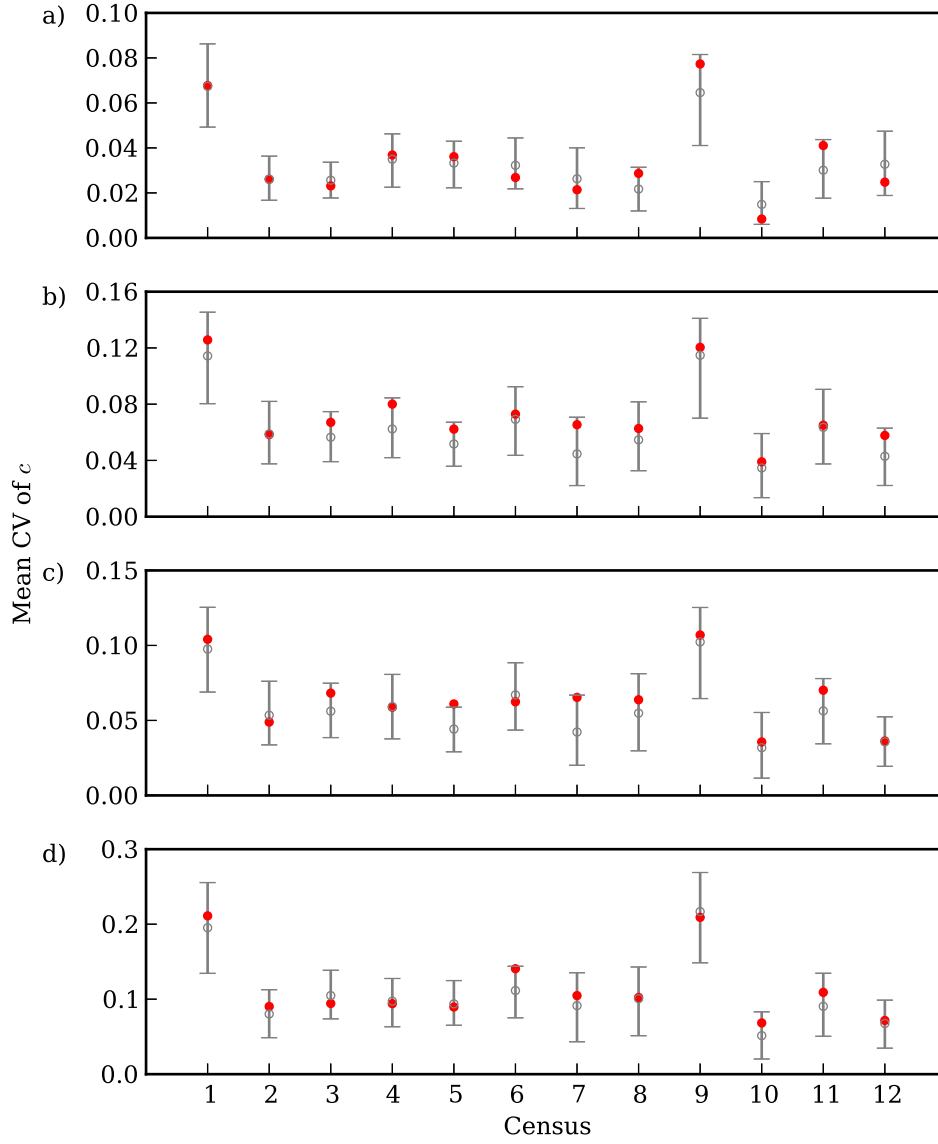


Figure 5.15: Results of the shoal randomisation test. For a colour variable c , the coefficient of variation (CV) of c was calculated for every shoal caught in a census. The mean CV of c over all the shoals in a census was taken as the test statistic and is plotted with filled red circles. The distribution of this test statistic obtained from the randomisation procedure is represented as an open grey circle at the median and error bars extending from the 2.5–97.5th percentiles. The figure shows the results for a) surface area (SA), b) total coloured area (TC), c) percentage coloured area (PC) and d) area covered by red, orange or yellow (ROY).

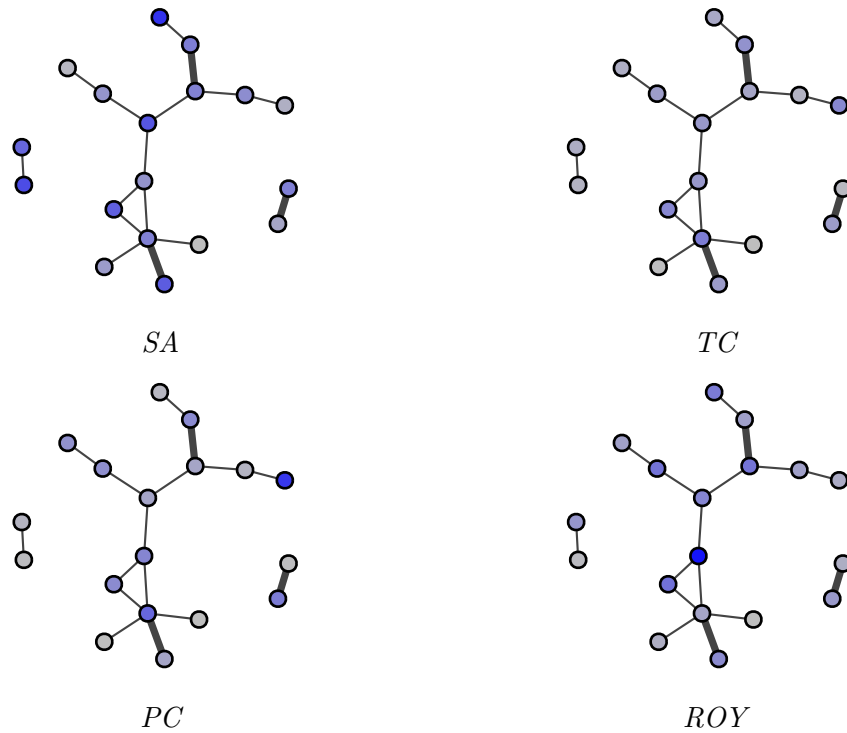


Figure 5.16: The social network of male guppies filtered to $X \geq 2$. Nodes are coloured according to colour attribute (c) a) SA, b) TC, c) PC & d) ROY on a scale from grey to blue representing the minimum and maximum values of the c respectively. Isolates have been removed.

there is colour data. Table 5.1 shows the distribution of X for these males. There were just 16 pairs of males which were found together more than once.

| X | 1 | 2 | 3 |
|-----------|-----|----|---|
| frequency | 186 | 13 | 3 |

Table 5.1: Distribution of X for males with colour data.

The network of repeated associations ($X \geq 2$) between males is shown in Figure 5.16. A network has been drawn for each of the four colour attributes c with the node colour varying from grey to blue according to the value of c . Assortment by c could be indicated if for example strongly coloured blue nodes have network neighbours which also have a high saturation of blue. In fact there is no clear evidence of this from visual inspection. This does not however preclude the possibility of assortment and therefore this was checked using quantitative analysis.

To test if males on average shoal with other males less brightly coloured than

themselves, the correlation between each male's colour attribute (c_i) and the mean colour attribute of its k network neighbours was calculated as

$$\frac{\sum_{j=1}^k X_{ij}c_j}{\sum_{j=1}^k X_{ij}}.$$

This was repeated for each of the four colour attributes. The correlation was strongest for TC and PC (Fig. 5.17c & e) with correlation coefficients of $\rho = -0.45$ and $\rho = -0.38$ respectively. The correlation was weaker for SA ($\rho = -0.31$) (Fig. 5.17a) and no correlation was seen for ROY ($\rho = 0.021$) (Fig. 5.17g).

The significance of each correlation was tested using the group randomisation method. In this analysis only the shoal assignments of the males with colour data were randomised so as to preserve the number of males per shoal and the degree distribution of the resultant male-male network. 10,000 randomised shoal compositions were created and a correlation coefficient ρ calculated for each randomisation to yield a distribution of ρ . The observed value of ρ was then compared to the calculated distribution to assess its significance (Fig. 5.17). A significant negative correlation between colour attribute and mean colour attribute of network neighbours was found for TC and PC (Fig. 5.17d & f) but not for SA or ROY (Fig. 5.17b & h). These significant correlations suggest that amount of colour may be a contributing factor towards the structure of the male-male social network.

5.8.3 Discussion

Sexual selection favours males guppies which are more brightly coloured (Kodric-Brown 1985). Males compete amongst themselves for access to females and it has been shown that females discriminate amongst males based on their colour (Kodric-Brown 1985). It is therefore possible that colour could play a role in structuring male-male associations. For example males may try to shoal with other males less colourful than themselves in order to make themselves appear more attractive.

Four measures were used in order to quantify the colouring of males – surface area (SA), total coloured area (TC), percentage coloured area (PC) and the area

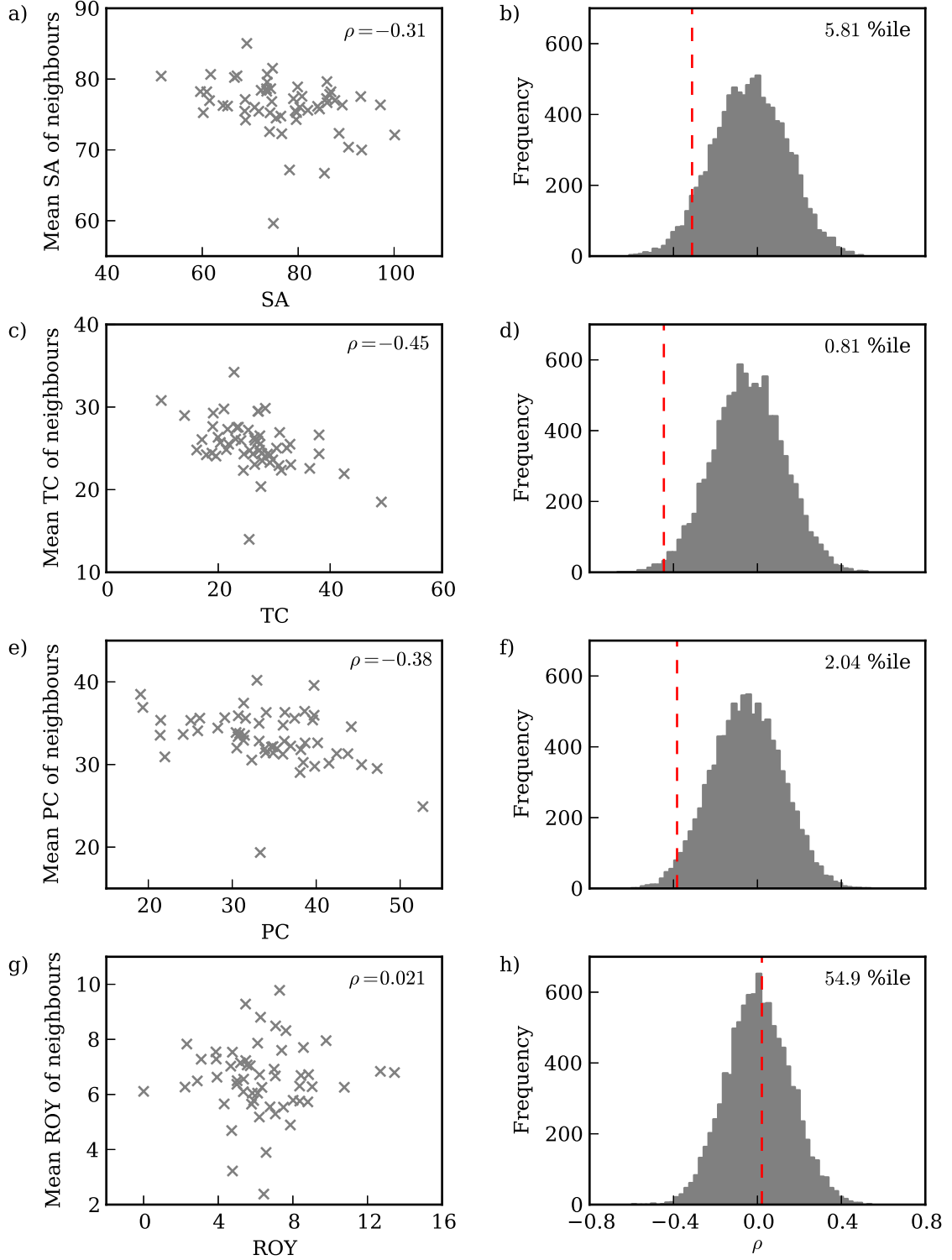


Figure 5.17: Plots on the left show the relationship between a node's colour attribute c and the mean c of its k network neighbours ($\langle c \rangle_k$) (a), c), e) & g)). Plots on the right show the distribution of the correlation coefficient of the corresponding left hand plot produced from 10,000 randomisations of the data. The observed correlation coefficient is shown by the dashed red line. Colour attributes shown are SA (a) & b)), TC (c) & d)), PC (e) & f)) and ROY (g) & h)).

coloured red, orange or yellow (ROY). Assortment by each of these measures was looked for both at shoal and network level.

Analysis at shoal level was carried out for each census separately to avoid pseudo-replication of data points. The mean coefficient of variation (CV) of a colour variable for each shoal in a census was used as the test statistic. Assortment of shoals by colour means that there would be shoals containing mainly brightly coloured males and shoals containing mainly less colourful males. This would result in the mean CV of a colour variable being smaller than expected by chance. However the observed mean CV for all colour measures was never less than expected by chance. There was also no consistency in whether the test statistic was higher or lower than the median value of the randomisation distribution. It is therefore concluded that the shoals were not assorted by colour.

Assortment at the network level was tested by calculating the correlation between a colour attribute of a male and the mean colour attribute of its network neighbours. If males seek to be close to other males less colourful than themselves this could lead to the colour of males being negatively correlated with the mean colour of their network neighbours. A significant negative correlation was found for TC ($\rho = -0.45$, $P = 0.0081$) and PC ($\rho = -0.38$, $P = 0.0204$) but not for SA or ROY. These findings suggest that colour could play a part in structuring male-male social networks. It is however important to remember that the existence of a correlation is not evidence of causality and the correlation itself does not provide information about the process by which this structure has come about. It may be that male guppies actively try to shoal with other guppies who are less brightly coloured than themselves or there may be some other process producing the same result. This is the first study to consider male guppy colour in the context of the social network and so further studies on different populations would strengthen this result.

Chapter 6

Association indices for open populations

Association indices (AIs) are used to quantify the level of association between each pair of animals in a study. More specifically, they aim to estimate the probability that two animals are found associating (p) (Cairns and Schwager 1987, Ginsberg and Young 1992). Estimation of p is not straightforward since in most studies animals will be observed differing numbers of times. AIs can be designed to tackle this by standardising the number of observations by some measure of effort (Whitehead 2008b). This chapter considers open populations where animals can and do leave the study area.

For the case of sparse association data, typical SNA proceeds as following. First observations of group membership are recorded (Sec. 4.1). From these the network is constructed, using an AI to calculate edge weights. Lastly some feature of the network structure is tested, usually by means of a randomisation test (Sec. 4.3). This last step is crucial for sparsely-sampled populations, as network structure can be strongly influenced by variation in the number of times an animal is observed, the distribution of group sizes and so on. Nonetheless, the assessment of the network structure is made before this step. If the AI does not accurately portray the social structure we may either miss the most interesting features to test for or possibly reach false conclusions. It is therefore paramount that the AI does the best possible job of quantifying network structure.

In group based studies observations of pairs of animals (a, b) are classified into 5 types: a and b seen in the same group, a and b seen in different groups, a observed and b not (or vice versa) and neither a nor b observed. The total counts of these observations are known as X , Y_{ab} , Y_a (Y_b) and Z respectively (Table 6.1) and all of these can be helpful in estimating p .

| Definitions | |
|-------------|---|
| X | Number of times animals a and b are observed in the same group. |
| Y_{ab} | Number of times a and b are both seen, but in different groups. |
| Y_a | Number of times a is seen but not b . |
| Y_b | Number of times b is seen but not a . |
| Z | Number of times neither a nor b is seen. |
| T | Total number of censuses. |

Table 6.1: *Notation definitions for ratio indices.*

The simplest AI is X . This is not strictly an estimator of p (since X takes integer values and can be greater than 1) but can easily be converted by dividing by T . The difficulty with using X is that when there is large variation in the numbers of times animals are observed X becomes highly correlated with the observation frequency and therefore is not such a good indicator of association strength. To ameliorate the problem a family of ‘ratio’ indices has been developed, each of the form $X/f(X, Y_{ab}, Y_a, Y_b, T)$. Different ratio indices work better for different sampling biases and these will be discussed in Section 6.1. Ratio indices are a practical choice for calculation as they require no additional information other than the observations of group membership.

When selecting which ratio index to use many studies refer to Cairns and Schwager (1987), a study comparing the performance of three ratio indices (the Simple Ratio Index (SRI), Half Weight Index (HWI) and Twice Weight Index (TWI)) under different sampling biases. Cairns and Schwager (1987) demonstrates that the performance of different indices varies depending on whether animals are more likely to be observed when together or apart. This was shown using a simulation which allowed the sampling bias to be varied in a controlled way. Cairns and Schwager (1987) also developed two idealised models for which maximum likelihood estimators (MLEs) could be derived. MLEs are mathematical formulae for

the most likely value of p for a given set of observations (in this case group memberships). Group observations were simulated using the idealised models and the MLEs used as ‘gold standards’ against which to compare traditional ratio indices and hence evaluate their performance. These results were used to make recommendations regarding the choice of ratio index in real studies. MLEs are not generally used in practice as they tend to be mathematically intractable for a real scenario, to require assumptions to be made or to require additional information about the system. Nevertheless Cairns and Schwager (1987) recommends considering whether an MLE can be derived for a specific study rather than immediately selecting an ‘off the shelf’ index. Nearly 30 years have passed and only a few studies have attempted this (Klaich et al. 2011 being an exception).

The work in this chapter has been primarily motivated by the Trinidadian guppy (*Poecilia reticulata*) study described in the previous chapter. The sampling scenario used there includes a feature not considered in Cairns and Schwager (1987), namely that animals can and do leave the study area. In the guppy study, entire shoals of guppies were captured from a natural pool in a section of a river. Guppies left and returned to the study pool and it was found that the emigration rate of males was almost twice that of females (the average number of marked males and females caught per day decreased by 46 % and 26 % respectively between the first 3 and final 3 study days (Sec. 5.4)). The marked guppies used for the study were part of a far larger number of guppies inhabiting the river and there was no segregation between marked and unmarked fish.

Consideration of the guppy study lead to the idea that associations ‘inside’ the study area may be different from those ‘outside’. Inside the study area, in this case the natural pool, guppies have the opportunity to associate with other marked guppies. The pool was small enough for guppies to swim across it in tens of seconds. This, combined with the rapid fission-fusion nature of shoals, meant that there was ample time for shoal memberships to be reconfigured between censuses. In contrast the space outside the study area, the rest of the river, is much larger and the majority of guppies there will be unmarked. It therefore seems much more unlikely that marked fish will associate when outside the study area as they are far less likely to encounter each other.

The work in this chapter aims to extend the ideas in Cairns and Schwager (1987) to include the case where animals can be outside the study area. Following the

structure of Cairns and Schwager (1987) I first develop an idealised model of the sampling scenario, and for this model I derive an MLE which I refer to as EB1. On my idealised model I compare the performance of the two most popular ratio indices with EB1 whilst varying a parameter q , the probability that an animal will be inside the study area, in order to justify the use of different ratio indices for different values of q . I use the results to formulate a new AI (called the ‘ q -weighted index’ or QWI) which aims to perform better than other ratio indices when animals can be outside the study area. Networks are then built with QWI, SRI and HWI for the guppy data and these show marked structural differences. Prior to this main body of work I begin by reviewing existing AIs.

6.1 Review of existing AIs

AIs originated in the field of ecology and were used to measure the co-occurrence of species in space (Ginsberg and Young 1992). An area would be subdivided into smaller ‘transect sites’ and AIs were used to measure the number of sites in which species a and b were found as a proportion of the total number of sites in which a (or b) was found (Dice 1945). In the context of ASNs, all AIs are estimators (\hat{p}) of the probability of finding animals a and b in the same group (p).

Maximum likelihood estimators

MLEs are a way of calculating the most likely value of p for a given set of observations. As such in general they outperform all other indices. MLEs are derived by writing down a likelihood function which describes the probability of observing a specific outcome (set of values for X , Y_{ab} , Y_a , Y_b and Z) as a function of the underlying parameter p . The value of p which maximises this function is the most likely value for p .

To derive an MLE a model of the sampling protocol must be defined. In most cases it is impossible to construct a model which incorporates all the features of real systems and therefore assumptions and simplifications are made. Cairns and Schwager (1987) defined two models for group based studies each model

specifying that j out of k groups were observed in each census. In the first model j and k are held constant for each census. This definition allows an expression for the probability of each type of sighting (X, Y_{ab}, Y_a, Y_b, Z) to be written down and hence a likelihood function can be constructed. In this case the likelihood function is solvable and yields a \hat{p} in terms of $X, Y_{ab}, Y_a, Y_b, Z, j$ and k . Using a computer to simulate observations using their model Cairns and Schwager (1987) showed that their derived MLE is a less biased and more precise \hat{p} than both SRI and HWI (see below for definitions). Their second model modified the first by allowing one group to be observed with a different probability from the others. A simulation using this model also found the MLE to perform better than SRI and HWI.

Klaich et al. (2011) developed a different model for deriving an MLE. Instead of parameterising how many groups are observed, Klaich et al. (2011) based their model on the probability of observing each individual. This probability was allowed to vary between individuals and between different sampling occasions and was also dependent on whether the individual was found to be associating or not. The likelihood equation formulated from this model contains $T[N(N-1)/2 + 2N]$ parameters for a study with N individuals and T sampling occasions which could not be fitted in practice (Klaich et al. 2011). Instead Klaich et al. suggest ways of simplifying their model to greatly curtail the number of parameters by reducing the degrees of freedom of the observation probability. Like Cairns and Schwager (1987), Klaich et al. (2011) demonstrates their MLE to be more accurate than SRI and HWI through use of a simulation. Klaich et al. (2011) also demonstrate the application of their MLE on a real data set (a population of Commerson's dolphins (*Cephalorhynchus commersonii*) in the Patagonian Northern Sea).

Whilst it is appealing that MLEs outperform traditional ratio style indices, there are difficulties in using MLEs in practice. MLEs often make assumptions which are unrealistic; for example both of Cairns and Schwager's models assume that j and k are the same in every census. In addition MLEs often require information not included in group observations. Cairns and Schwager's models also require the value of k to be known. For these reasons, MLEs are seldom used. The remainder of this section describes commonly used alternatives to MLEs.

A simple count

The simplest way to weight network edges is to count occurrences of association. For group based studies this measure is usually called X and refers to the number of times two animals are observed in the same group. In order to achieve a scale between 0 and 1 the count can be divided by the total number of observation periods T to give the proportion of periods in which joint group membership is observed. X was used in the previous chapter as a measure of association strength between pairs of guppy fish.

Ratio indices

The difficulty with using a simple count as a measure of association strength is that in most studies each animal is observed a different number of times. For example, a pair of animals observed together twice would have the same association strength ($X = 2$) as a pair observed together twice and in different groups four times. A better indicator of association would be the fraction of associations which each animal spends with another animal. Ratio indices attempt to estimate this by dividing X by some function $f(X, Y_{ab}, Y_a, Y_b, T)$. However for reasons described in the following paragraph, this fraction is not so straightforward to estimate.

If animals a and b are observed a different number of times, then the fraction of observations of a in which a is associating with b ($X/(X + Y_a + Y_{ab})$) is not the same as the fraction of observations of b in which b is associating with a ($X/(X + Y_b + Y_{ab})$) since $Y_a \neq Y_b$ (Ginsberg and Young 1992). There does however exist a true single amount of time that a and b spend associating and the difference in the fractions results from bias introduced by uneven sampling (Ginsberg and Young 1992). The denominator in ratio indices (f) serves to reconcile the difference between $X/(X + Y_a + Y_{ab})$ and $X/(X + Y_b + Y_{ab})$ producing a symmetric index to give the best possible estimate of p . Since there is no perfect way to do this and all ratio indices are biased in some way a range of ratio indices have been developed each to suit a different purpose. The specific biases introduced at the sampling stage (for example if for many pairs $Y_a \gg Y_b$) influence the choice of index. Table 6.2 defines some well known ratio indices

each of which will be described in turn in this section.

| Index | Ratio indices of the form $\frac{X}{f(X, Y_{ab}, Y_a, Y_b, T)}$ |
|--------------------------|---|
| Proportion | T |
| Simple Ratio Index (SRI) | $X + Y_{ab} + Y_a + Y_b$ |
| Half Weight Index (HWI) | $X + Y_{ab} + \frac{1}{2}(Y_a + Y_b)$ |
| Twice Weight Index (TWI) | $X + 2Y_{ab} + Y_a + Y_b$ |
| Square Root Index (SQI) | $\sqrt{(X + Y_a + Y_{ab})(X + Y_b + Y_{ab})}$ |
| Both Identified (BI) | $X + Y_{ab}$ |
| Social Affinity (S) | $\min((X + Y_{ab} + Y_a), (X + Y_{ab} + Y_b))$ |

Table 6.2: Association indices which take a ‘ratio’ form.

The first index listed (Proportion) was mentioned in the previous subsection and does not correct any bias which may be present in X . The Square Root Index (SQI) developed by Lott and Minta (1983) has been shown to be based on a flawed probability model (Cairns and Schwager 1987) and so will not be considered further here. The most widely used indices are the Simple Ratio Index (SRI), Half Weight Index (HWI) and Twice Weight Index (TWI) (Whitehead and Dufault 1999, Cairns and Schwager 1987). The SRI measures the number of censuses in which two animals are found to be associating as a fraction of the total number of censuses in which at least one of them is observed. The HWI is similar except it gives half as much weight to censuses in which only one animal is observed. The TWI differs from the SRI by giving twice as much weight to censuses in which the animals are observed in separate groups. All three of these indices have been used to study a wide range of species e.g. SRI: yellow-bellied marmots (Nanayakkara and Blumstein 2010), African elephants (*Loxodonta africana*) (Chiyo et al. 2011) HWI: sperm whales (*Physeter macrocephalus*) (Gero et al. 2013), Australian snubfin (*Orcaella heinsohni*) and Indo-Pacific humpback dolphins (*Sousa chinensis*) (Parra et al. 2011) TWI: spotted hyenas (*Crocuta crocuta*) (Holekamp et al. 1997).

In cases where every animal is observed in each census ($Y_a = Y_b = Z = 0$) the SRI and HWI reduce in form to become the same as the BI (Cairns and Schwager

1987). This scenario is most likely to occur in lab based experiments where the animals are confined. If the animals are never found in separate groups ($Y_{ab} = 0$) the SRI and TWI are the same (Cairns and Schwager 1987). However in most studies $Y_a, Y_b, Y_{ab} \neq 0$ therefore each index yields a different value. The HWI and TWI are monotonic functions of each other so the ranking of edges by weight will be the same for both (Cairns and Schwager 1987). In contrast the SRI is not a monotonic function of either the HWI or TWI (Cairns and Schwager 1987). This means that the ranking of edges depends on the choice of index and therefore the outcome of statistical tests based on these indices may be different (Cairns and Schwager 1987).

Cairns and Schwager (1987) showed that the relative accuracy of the SRI, HWI and TWI depends on the sampling bias. They considered the bias introduced when there is a difference in observation probability depending on whether or not animals are associating. Their conclusion, based on a simulation in which a pair's probability of observation was allowed to vary, is that the HWI is least biased when pairs are more likely to be observed when they are not associating, the TWI is least biased when the reverse is true, and the SRI is least biased when there are no differences in observation probability. They did not test the lesser used BI and so its performance under this bias is unknown.

The Social Affinity index S (Table 6.2) was proposed by Lazo (1994) to deal with a different bias. Lazo's study on Doñana feral cattle (*Bos taurus*) involved observing groups of cattle sequentially from a car or on horseback over a period of 3 years. S was calculated as the number of times a and b were located in the same group divided by the minimum of the number of times a was seen and the number of times b was seen. Lazo (1994) justified his use of S by saying it is insensitive to any difference between the observation probabilities of a and b . This assertion was not however backed up with any evidence.

Modified counts and ratio indices

Godde et al. (2013) proposed a modification to the HWI in order to compensate for differences in gregariousness among individuals. Node strength (the sum of the weights of all edges attached to a node) can be large either because of an individual having a large number of social partners (a consequence of gregarious-

ness) or because of an individual having strong social preferences. If the aim is to ascertain individuals' propensities to form social preferences it is not desirable that node strength does not differentiate between this and gregariousness. Godde et al. calculate their new index, the HWIG, by multiplying each element of the HWI by a scaling factor dependent on the combined gregariousness of the two individuals

$$\text{HWIG}_{ab} = \text{HWI}_{ab} \frac{\sum \text{HWI}}{\sum \text{HWI}_a \sum \text{HWI}_b},$$

where HWIG_{ab} is the value of HWIG between animals a and b , HWI_{ab} is the value of HWI between animals a and b , $\sum \text{HWI}$ is the sum of the HWI between all pairs of animals and $\sum \text{HWI}_{a,(b)}$ is the sum of the HWI between a (b) and all other animals. Using a simulation Godde et al. (2013) showed that the HWIG is less influenced by gregariousness than the HWI and they recommend using the HWIG for populations where there is a range of gregariousness. The same correction could also be applied to any of the other ratio indices and Godde et al. (2013) found the same results when testing the SRI, TWI and SQI.

In the context of scientific collaboration networks, Newman (2001) suggested what is in effect a modification to X for group based data. In scientific collaboration networks edges are placed in the network between all scientists who co-authored a particular paper so that each paper is analogous to a group in a biological network. Newman posits that if there are many authors on a paper then the association strength between the authors is less than on a paper with only a few authors. He suggests the edge strength added for each paper should be modified from 1 (as it would be under X) to $\frac{1}{n-1}$. This makes the total weight of an edge w_{ij} equal to

$$w_{ij} = \sum_k \frac{\delta_i^k \delta_j^k}{n_k - 1},$$

where δ_i^k is 1 if scientist i was a co-author on paper k and zero otherwise and n_k is the number of authors of paper k . For studies where the biologist believes associations between animals in large groups to be weaker than ones in small groups this modification to X could be a useful way of compensating for the differences. It is worth noting however that when using this modification the node strength becomes equal to the number of groups in which the animal was found (Newman 2001).

Other indices

An alternative method for analysing group living animals was proposed in Cross et al. (2005). They argue that group compositions of African buffalo (*Syncerus caffer*) are the result of fission and fusion events and look to see if there is structure in the choices individuals make regarding which other individuals to remain with following a fission event (splitting of a group). They propose a new AI called the fission decision index (FDI) which is defined as the number of times animals a and b were together after a fission event divided by the total number of fission events involving both animals. This is given by the formula

$$\delta_{ab} = \frac{T_{ab}}{T_{ab} + A_{ab}}$$

where T_{ab} is the number of times animals a and b were together after a fission event and A_{ab} is the number of times a and b were apart after a fission event.

The FDI necessitates using a different sampling protocol (Cross et al. 2005). In order to assess group configurations before and after every fission event observations of group memberships must be taken initially and then once after every fission event. This is in contrast to traditional sampling methods which often involve taking observations at regular time intervals. Cross et al. point out that if sampling occurs more regularly than fission and fusion events then successive observations will be autocorrelated and this may lead to false positive results from significance tests. Cross et al. present their FDI index as a solution to this problem.

For a case where association is inferred from shared space use, Gygax et al. (2010) proposed an index they call *synchronicity*. For their study on dairy cattle they divided a barn into three functional areas: activity, feeding and lying. The synchronicity, measured for each functional area in turn, was defined as the number of observations in which two cows were in the same functional area divided by the number of observations in which both cows were observed and at least one of the cows was in the same functional area in question (Gygax et al. 2010). This current definition of synchronicity is specific to this particular study and so may have limited applicability elsewhere.

6.2 Sampling open populations

In this chapter I will consider the case where animals associate only when they are inside the study area. This could be because the area outside the study area is so large that animals are unlikely to encounter each other, or because there are so many other animals outside the study area that again study animals would be unlikely to meet. This is most relevant for systems such as the Trinidadian guppy in which groups have rapid fission-fusion dynamics relative to the frequency of leaving and returning to the study area. This case would not be applicable to systems where animals maintain longer lasting group compositions such as pack animals where group compositions would be expected to remain mostly unchanged whether the animals are within the study area or not.

To formalise the separation between inside and outside the study area, I propose breaking down the AI depending on the location of the animals. I introduce the idea of a ‘global’ index (GI) which estimates the unconditional probability that two animals will be found together. I also introduce a ‘local’ index (LI) which estimates the probability that two animals will be found together given that they are both in the study area. GI and LI are linked using the equation

$$GI = SF \times LI$$

where SF is a spatial factor which is the probability that both animals are inside the study area.

6.2.1 Four sampling scenarios

Figure 6.1 shows four possible sampling scenarios which will be referred to in the rest of this chapter. In each scenario the study area is the region inside the large circle. This is the maximum extent of each survey, transect or census of the population. Animals are represented by small circles and their status is indicated by their colour: observed (black), inside the study area but not observed (white) or outside the study area (grey). It is assumed that the study area is sufficiently small that all observed animals (black) could have associated with all others (black or white) within the study area during a census, but not with those

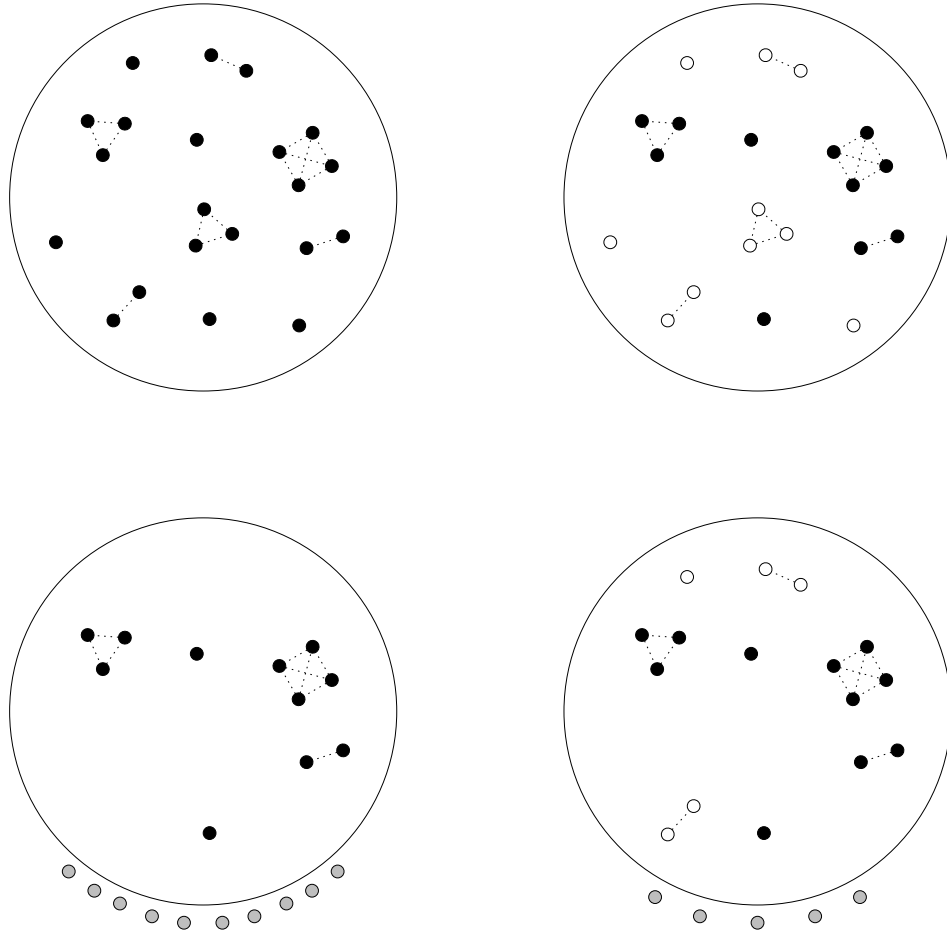


Figure 6.1: Four possible sampling scenarios. The area enclosed by the large circle represents the study area. Animals are represented by small circles. All animals in a group are connected by dotted lines. Animals which are observed are filled black, unobserved animals inside the study area are filled white and animals outside the study area are filled grey. a) Scenario A: Closed system with complete sampling. All animals are inside the study area and all animals are observed. b) Scenario B: Closed system with incomplete sampling. Animals are confined to the study area but not all animals are observed. c) Scenario C: Open system with complete sampling. Animals are able to leave the study area. d) Scenario D: Open system, incomplete sampling. Animals are able to leave the study area and not all animals within the study area are observed.

outside (grey).

The study area is either closed (all animals remain inside, Fig. 6.1a & b) or open (Fig. 6.1c & d). In addition the sampling of animals in each census is either ‘complete’ (all animals within the study area are observed Fig. 6.1a & c) or incomplete (Fig. 6.1b & d). The particular interest of this chapter is Scenario D (Fig. 6.1d). In this case we do not know whether an unseen animal is inside or outside the study area. We can however make probabilistic arguments based on what we know about how each animal uses the space.

Scenario A: Closed population, complete sampling

Figure 6.1a shows the simple case where all animals are confined to the study area and every animal is observed in each census. This situation is most likely to occur for captive populations. In this case $GI = LI$ as all animals are always in the study area. The simple proportion X/T (Table 6.2) is the MLE for both GI and LI . In this scenario $Y_a = Y_b = 0$ and $X + Y_{ab} = T$; therefore all the ratio indices are equivalent $X/T = HWI = SRI = BI = TWI$.

Scenario B: Closed population, incomplete sampling

Figure 6.1b shows the case where all animals are confined to the study area but not all animals are observed in each census. This includes situations where in each census the observation is limited to a fixed part of the study area, a fixed number of animals or a fixed number of groups. This scenario could occur when animals are restricted spatially, for example they may be living on an island but not all of the island is observed. As in Scenario A, $SF = 1$ and $GI = LI$. In contrast to Scenario A, observation frequencies of animals will vary. Even in this relatively simple scenario it is difficult, if not impossible, to derive an MLE as we do not know anything about the number and size of the unobserved groups. In this case most authors use one of the ratio indices (typically SRI or HWI) to take some account of unobserved (white) individuals.

Scenario C: Open population, complete sampling

In Figure 6.1c all animals within the study area are observed but some animals (grey) may be outside the study area. In any one census animals inside the study area do not have the opportunity to associate with animals outside the study area. It is also assumed that animals outside the study area do not associate with each other.

Scenario D: Open population, incomplete sampling

Many studies fall into the most problematic of the scenarios depicted in Figure 6.1d. Observations of large mammals in national parks (Lazo 1994), marine mammals (Whitehead and Rendell 2004) and fish in streams (Ward et al. 2002, Croft et al. 2004b) are examples. In each census unobserved animals may be either inside (white) or outside (grey) the study area. When only one animal of a pair (a , b) is observed, it is unknown whether the unobserved animal was inside the study area (a could have associated with b) or outside (a and b could not have associated). As for Scenario B, most studies use one of the ratio indices to avoid discarding information obtained in censuses where only one animal of a pair is observed (Y_a or Y_b). In this scenario, $SF < 1$ and $GI < LI$.

6.3 Deriving an MLE for an idealised model

In this section I define a model in which animals can be outside the study area. This will be an extension of Cairns and Schwager's Model 1 (Cairns and Schwager 1987). Their model specifies that in each census j out of k groups are observed. All k groups contain the same number of animals and are equally likely to be observed. j and k are the same for every census. Their sampling scenario is equivalent to Scenario B where all animals are inside the study area. Each pair of animals has the same probability of being in the same group in every census, which effectively means there is no concept of 'outside the study area' in this model.

In order to extend this model to incorporate Scenario D, I introduce an extra parameter q , the probability of an animal being inside the study area during each census. q is the same for all censuses. In my model I assume that animals outside the study area are not associating with each other. This may not be entirely true for a real situation but I aim to show that this assumption may affect the choice of AI. The concept of k groups inside the study area of which j are observed is retained. The parameters used for my model are summarised in Table 6.3. The parameter values corresponding to the four scenarios described in the previous section are shown in Table 6.4.

| Model parameters | |
|------------------|---|
| k | Number of groups inside the study area. |
| j | Number of observed groups. |
| q | Probability of an animal being inside the study area. |
| T | The number of censuses. |

Table 6.3: *Summary of model parameters used in my idealised sampling model (Sec. 6.3).*

| Scenario | q | j/k |
|----------|-------|-------|
| A | 1 | 1 |
| B | 1 | < 1 |
| C | < 1 | 1 |
| D | < 1 | < 1 |

Table 6.4: *Parameter combinations corresponding to the four sampling scenarios depicted in Figure 6.1.*

Cairns and Schwager developed an MLE for their Model 1 which I will refer to as CS1. In Section 6.3.1 I develop a corresponding MLE for my model which I will refer to as EB1. I then use a simulation similar to the one used by Cairns and Schwager to compare the performance of EB1 and CS1 against the most frequently used ratio indices HWI and SRI.

6.3.1 Derivation of EB1

EB1 is an estimator for the unconditional probability p that two animals will be in the same group. This MLE is derived using the likelihood equation

$$\mathcal{L}(\theta|x) = P(x|\theta) \quad (6.1)$$

where $\mathcal{L}(\theta|x)$ is the likelihood of a set of parameter values θ given an observation set x and $P(x|\theta)$ is the probability of observing x as a function of the parameter θ (Held and Bov 2013). In this case there is just the single parameter p and the observations are X, Y_a, Y_b, Y_{ab} and Z . The expression that gives the most likely value for p can be found by maximising \mathcal{L} with respect to p .

In order to find $P(X, Y_a, Y_b, Y_{ab}, Z|p)$ it is necessary to write down the conditional probability of each type of sighting for a pair of animals a, b given according to whether a and b are in the same group (together) or apart. It is easiest to do this by breaking down the probabilities for the three scenarios: both a and b inside the study area, either a or b inside the study area and neither a nor b inside the study area. The probabilities for each case can then be written down using elementary combinatorics. For example the probability of recording an observation of X given that a and b are together is simply $\frac{j}{k}$ since j out of the k groups are observed. The constituent parts of the probabilities are shown in Table 6.5 and are combined for each conditional case in Table 6.6.

The expected values for each type of sighting can then be found by multiplying the conditional probabilities by either p or $(1 - p)$ depending on whether the condition is for the animals to be together or apart. The expected values for each type of sighting are shown in Table 6.7.

| | | Both inside | One inside | Both outside |
|----------|---------------------|---|---------------------------|--------------|
| Together | X | $\frac{j}{k}$ | - | - |
| | Z | $\frac{k-j}{k}$ | - | - |
| | $Y_a \text{ or } b$ | $q^2 \frac{j}{k} \frac{(k-j)}{(k-1)}$ | $q(1-q) \frac{j}{k}$ | - |
| Apart | Y_{ab} | $q^2 \frac{j}{k} \frac{(j-1)}{(k-1)}$ | - | - |
| | Z | $q^2 \frac{(k-j)}{k} \frac{(k-j-1)}{k-1}$ | $2q(1-q) \frac{(k-j)}{k}$ | $(1-q)^2$ |

Table 6.5: Probabilities of each type of sighting broken down by whether the animals are together or apart and by whether both, one or none are in the study area.

From the expected values, the likelihood function can then be written down as

$$\begin{aligned}
& \mathcal{L}(p; X, Y_a, Y_b, Y_{ab}, Z) \\
&= \binom{T}{X, Y_a, Y_b, Y_{ab}, Z} \left[\frac{j}{k} p \right]^X \left[q \frac{j}{k} \left[q \frac{k-j}{k-1} + (1-q) \right] (1-p) \right]^{Y_a+Y_b} \\
& \quad \times \left[q^2 \frac{j}{k} \frac{(j-1)}{(k-1)} (1-p) \right]^{Y_{ab}} \\
& \quad \times \left[\frac{k-j}{k} p + q^2 \frac{(k-j)}{k} \frac{(k-j-1)}{k-1} (1-p) \right. \\
& \quad \left. + 2q(1-q) \frac{(k-j)}{k} (1-p) + (1-q)^2 (1-p) \right]^Z.
\end{aligned}$$

where $\binom{T}{X, Y_a, Y_b, Y_{ab}, Z}$ is the product of the binomial coefficients for choosing X , Y_a , Y_b , Y_{ab} and Z from T .

Collecting all terms not dependent on p into a single term C and simplifying gives

$$\begin{aligned}
\mathcal{L} &= C p^X (1-p)^Y \\
& \quad \left(p \left[j(1+2q) + q^2 \left(k-2j - \frac{(k-j)(k-j-1)}{k-1} \right) \right] \right. \\
& \quad \left. + k-2jq + q^2 \left(2j-k + \frac{(k-j)(k-j-1)}{k-1} \right) \right)^Z \\
&= C p^X (1-p)^Y (up+v)^Z,
\end{aligned}$$

| Case | Probability |
|-------------------------------------|--|
| $p(X \text{together})$ | $\frac{j}{k}$ |
| $p(Z \text{together})$ | $\frac{k-j}{k}$ |
| $p(Y_a \text{ or } b \text{apart})$ | $q\frac{j}{k}\left[q\frac{k-j}{k-1} + (1-q)\right]$ |
| $p(Y_{ab} \text{apart})$ | $q\frac{j}{k}q\frac{j-1}{k-1}$ |
| $p(Z \text{apart})$ | $q^2\frac{(k-j)}{k}\frac{(k-j-1)}{k-1} + 2q(1-q)\frac{(k-j)}{k} + (1-q)^2$ |

Table 6.6: *Conditional probabilities of different types of sightings.*

where

$$Y = Y_a + Y_b + Y_{ab},$$

$$u = j(1 + 2q) + q^2 \left(k - 2j - \frac{(k-j)(k-j-1)}{k-1} \right), \quad (6.2)$$

$$\text{and } v = k - 2jq + q^2 \left[2j - k + \frac{(k-j)(k-j-1)}{k-1} \right]. \quad (6.3)$$

To derive the MLE we need to find an expression for p which maximises the likelihood function L . The easiest way to do this is to take the logarithm of L , differentiate it with respect to p and set it equal to zero. The value of p which maximises the logarithm of L will also maximise L . The logarithm of L is

$$\log L = \log C + X \log p + Y \log(1 - p) + Z \log(up + v),$$

and differentiating with respect to p gives

$$\frac{d}{dp} \log L = \frac{X}{p} - \frac{Y}{1-p} + \frac{uZ}{up+v}.$$

Here we see that the term C has dropped out since it does not depend on p .

| Type of sighting | Expected value |
|------------------|--|
| X | $\frac{j}{k}pT$ |
| Y_a or Y_b | $q\frac{j}{k}\left[q\frac{k-j}{k-1} + (1-q)\right](1-p)T$ |
| Y_{ab} | $q^2\frac{j}{k}\frac{(j-1)}{k-1}(1-p)T$ |
| Z | $\left[\frac{(k-j)}{k}p + q^2\frac{(k-j)}{k}\frac{(k-j-1)}{k-1}(1-p) + 2q(1-q)\frac{(k-j)}{k}(1-p) + (1-q)^2(1-p)\right]T$ |

Table 6.7: *Expected values of different types of sightings.*

Setting $\frac{d}{dp} \log L = 0$ gives

$$\begin{aligned}
0 &= \frac{X}{p} - \frac{Y}{1-p} + \frac{uZ}{up+v} \\
&= (1-p)(up+v)X - p(up+v)Y + up(1-p)Z \\
&= -u(X+Y+Z)p^2 + [(u-v)X - vY + uZ]p + vX \\
&= uTp^2 - [(u-v)X - vY + uZ]p - vX.
\end{aligned}$$

Solving for p gives the maximum likelihood estimator \hat{p} for p as

$$\hat{p} = \frac{w + \sqrt{w^2 + 4uvTX}}{2uT}, \quad (6.4)$$

where

$$w = (u-v)X - vY + uZ. \quad (6.5)$$

The formula for CS1 can be recovered from EB1 by using the parameter values for Scenario B. In Scenario B $q = 1$ and from Equations 6.2 and 6.3 we can see that $u = j$ and $v = k - j - 1$. Substituting these values into Equations 6.4 and

6.5 gives

$$\hat{p} = \frac{w + \sqrt{w^2 + 4jT(k - j - 1)X}}{2jT},$$

where

$$w = (2j - k + 1)X + (j - k + 1)Y + jZ, \quad (6.6)$$

which are the formulae for CS1.

6.3.2 Comparison of AI performance

A simulation was used to compare the performance of both EB1 and CS1 to commonly used ratio indices. Many ratio indices were investigated including HWI, SRI, TWI, BI and X/T but here results are shown only for HWI and SRI as these are the most commonly used and were also the best performing.

The simulation was conducted using the same method as used by Cairns and Schwager (1987). For a given combination of parameters (p, q, j, k) expected values of observations (X, Y_a, Y_b, Y_{ab}, Z) were calculated for one census (using $T = 1$) using the formulae in Table 6.7. For each census, a count for X, Y_a, Y_b, Y_{ab} or Z was incremented by comparing a random number generated by a uniform distribution $R \sim U(0, 1)$ to the range 0–1 divided into buckets proportionally according to the expected values of the observations. This procedure was repeated 10 times to simulate the total observations after 10 censuses. The values of each AI could then be calculated using the parameters and observation values.

The simulation was repeated 10^5 times for each combination of parameters (Table 6.8). The number of censuses was always kept at 10 since this is comparable to real studies (e.g. Croft et al. 2004b). The number of groups in the study area k was varied between 5 and 20 with $j \leq k$. q took values 0.5, 0.8 and 1 and p took values 0.2, 0.5 and 0.8.

The accuracy of an AI can be found by calculating the bias, defined as the difference between the value of the AI and p . This can be averaged over all 10^5 simulations (for one combination of parameters) to find the average bias. It is desirable for an AI to have both low bias and low variance (Whitehead 2008b). Low variance means that the spread of AI values will be small so that the value

| Parameter values | |
|------------------|--|
| $k : \{j\}$ | $20 : \{5, 10, 15, 20\}, 15 : \{5, 10, 15\}, 10 : \{5, 10\}, 5 : \{2, 3, 4, 5\}$ |
| q | 0.5, 0.8, 1 |
| p | 0.2, 0.5, 0.8 |
| T | 10 |

Table 6.8: *Parameter values used to generate simulated data for my idealised model.*

is more reliable in the presence of random variation.

Figure 6.2 compares the absolute bias and variance of CS1 with HWI and SRI. The data shown here are only for Scenario B (animals always in the study area, $q = 1$) so that the figure is comparable to Cairns and Schwager (1987) Figure 3, which plots the same variables for their corresponding simulation. The bias and variance of CS1 were found to be comparable to those of HWI (Fig. 6.2a & b). CS1 was much less biased than SRI with a similar variance (Fig. 6.2c & d). These findings agree with those in Cairns and Schwager (1987).

Figure 6.3 compares the absolute bias and variance of EB1 with HWI, SRI and CS1. These data include all parameter combinations. EB1 has a lower bias than HWI, SRI and CS1 for the majority of parameter combinations with SRI showing the poorest performance (Fig. 6.3 a, c & e). The variance of EB1 is similar to that of HWI, SRI and CS1 (Fig. 6.3 b, d & f).

The relationship between AI bias and parameters p , q and j/k is shown in Figure 6.4. In general over all parameter combinations EB1 is the least biased estimator of p (Fig. 6.4b). I have not calculated the average bias over all parameter combinations as the parameters do not cover the parameter space evenly and so the average would be meaningless. CS1 assumes that all unobserved animals associate to the same extent as observed ones and hence CS1 is always greater than EB1. The less time animals spend in the study area, the greater the disparity (Fig. 6.4d). For matching parameters HWI is always larger than SRI (Fig. 6.4a, c & e) since HWI always has a smaller denominator than SRI (Table 6.2). In the majority of cases HWI overestimates p whilst SRI underestimates p .

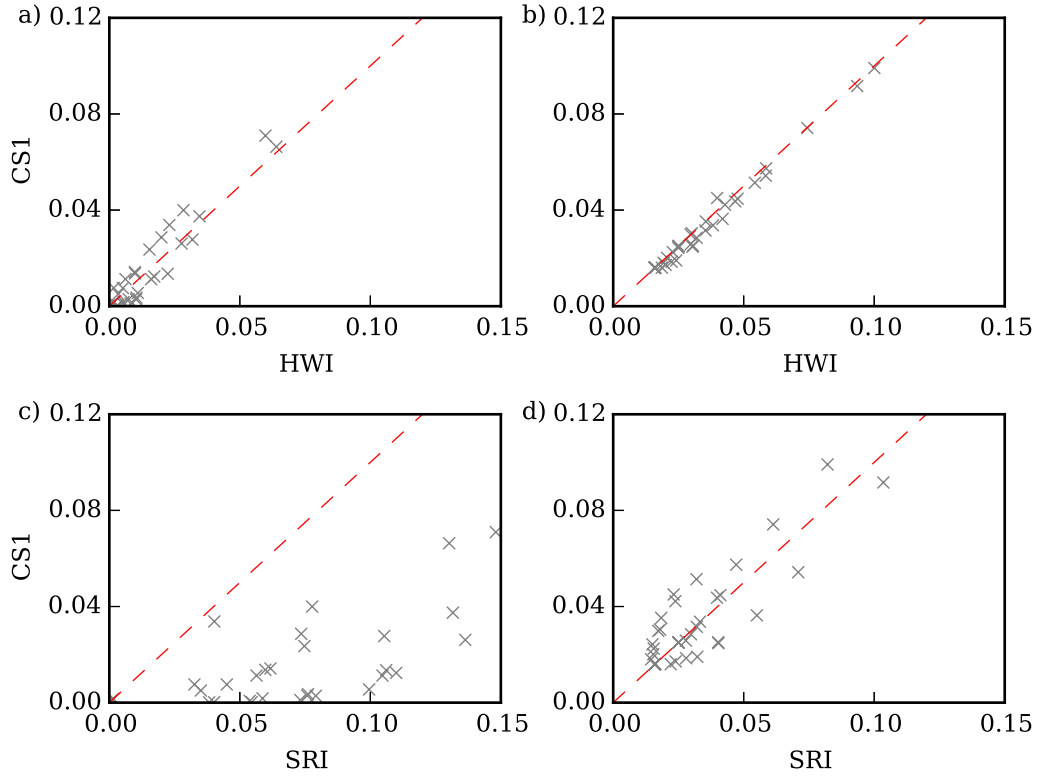


Figure 6.2: Comparison of the absolute bias and variance of CS1 with HWI and SRI. a) Absolute bias of CS1 compared with HWI. b) Variance of CS1 compared with HWI. c) Absolute bias of CS1 compared with SRI. d) Variance of CS1 compared with SRI. Each data point is the average over 10^5 simulations with a single combination of parameters. The red dashed line indicates the line $y = x$ so that points lying above the line show the bias or variance of CS1 to be greater than that of the other index and points lying below indicate that the other index has a greater bias or variance than CS1.

The expected behaviour is seen for the special cases of parameters which constitute Scenarios A, B and C. In Scenario C ($q < 1$, $j/k = 1$) both SRI and EB1 are unbiased (Fig. 6.4 e & f). For Scenario B ($q = 1$, $j/k < 1$) the formula for EB1 simplifies to CS1 and both indices yield the same values (Fig. 6.4d). In the simplest case of Scenario A ($q = 1$, $j/k = 1$) all indices simplify to BI and are unbiased estimates of p (Fig. 6.4c, d, e & f).

Whilst EB1 has proved to be less biased than conventional indices HWI and SRI it does have several drawbacks. Firstly it has been derived using an idealised model of animal groupings. The model requires all groups to be of the same size and also requires j and k to be the same for every census. In addition it is not

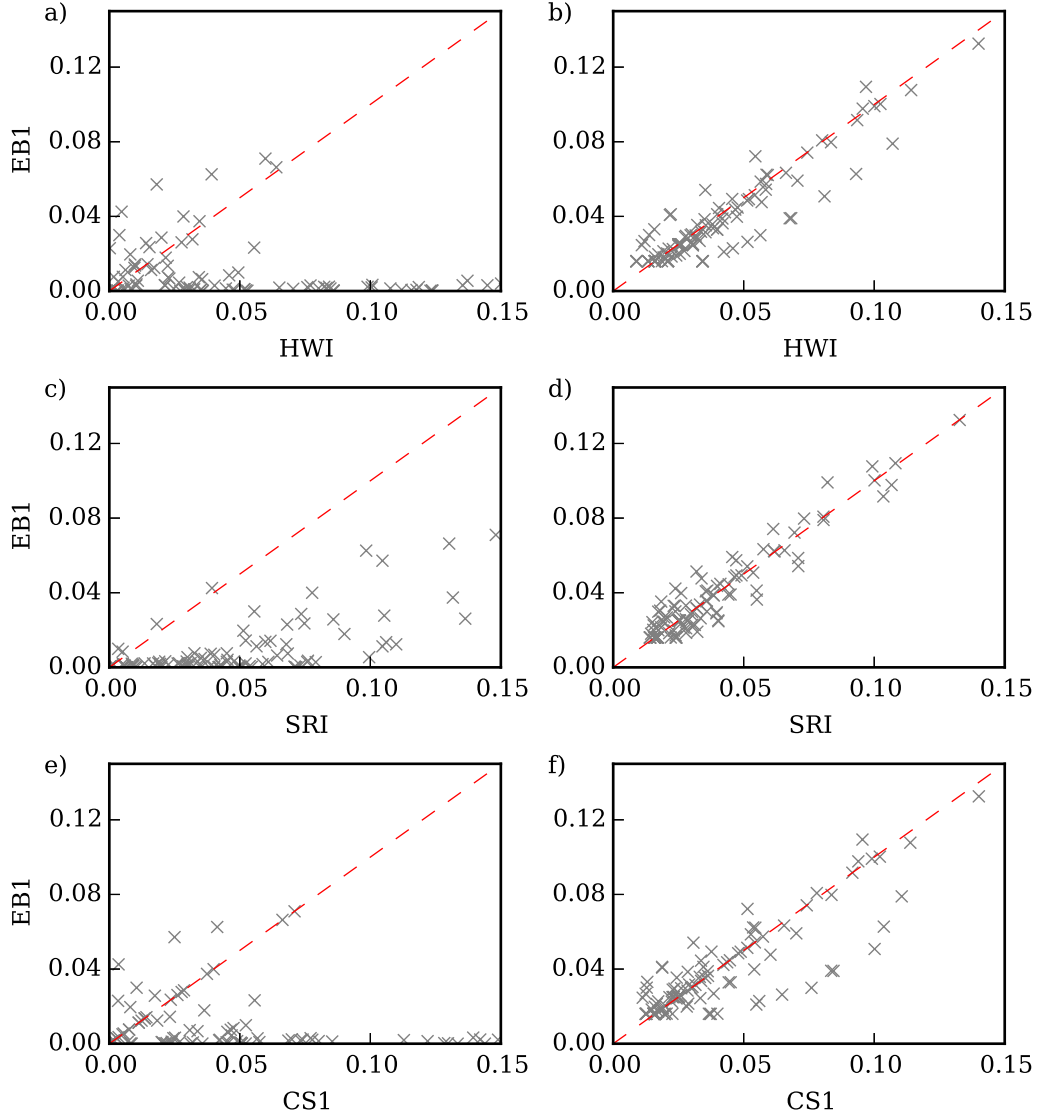


Figure 6.3: Comparison of the absolute bias (left hand column) and variance (right hand column) of EB1 with HWI, SRI and CS1. Each data point is the average over 10^5 simulations with a single combination of parameters. The red dashed line indicates the line $y = x$ so that points lying above the line show the bias or variance of CS1 to be greater than that of the other index and points lying below indicate that the other index has a greater bias or variance than CS1.

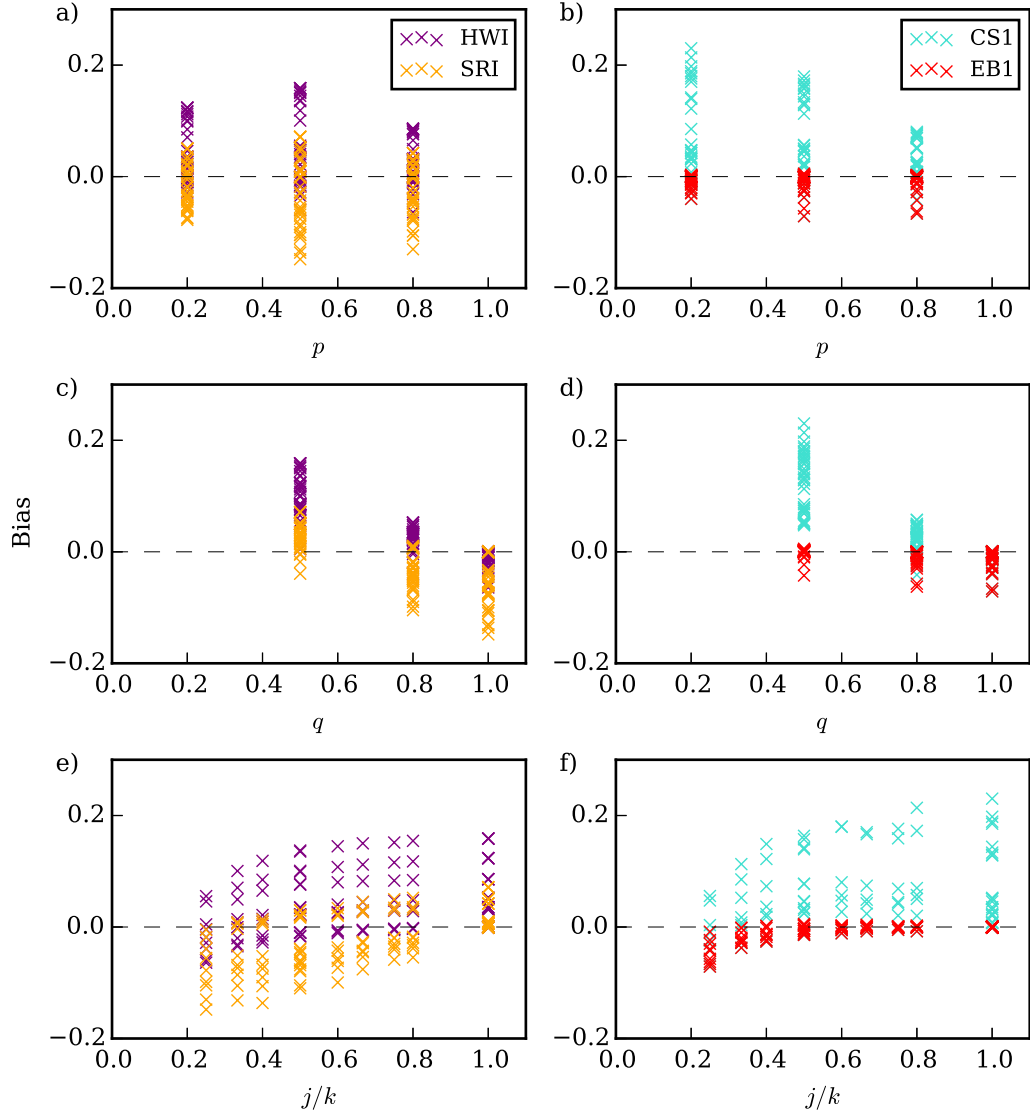


Figure 6.4: Variation of AI bias with parameters a) \mathcal{E} b) p , c) \mathcal{E} d) q and e) \mathcal{E} f) j/k . a), c) & e) Comparison of HWI and SRI bias. b), d) & f) Comparison of CS1 and EB1 bias.

possible to compute values for k and q from observations X , Y_a , Y_b and Y_{ab} and yet they are required in order to calculate EB1. Cairns and Schwager acknowledged these same difficulties for their index CS1. My model, whilst incorporating a broader range of sampling scenarios, has done so at the cost of introducing the extra parameter q .

Cairns and Schwager (1987) investigated the effect of using erroneous values of k on the accuracy of CS1. They found that large errors in k have only a small effect on CS1 and that the effect is particularly small for $j > 2$ and $k > 5$ (Cairns and Schwager 1987). I have not performed analogous sensitivity analyses which for my model are required for k and q . Such analyses could provide valuable information about how the accuracy to which k and q need to be estimated in order to apply EB1 to a real study.

The focus in the following section shifts from the simulated idealised model to the real data collected in the guppy study. I try to bridge the gap between the model and the real study by looking for an index inspired by the simulation results which is calculable when using real data.

6.4 Case study: Trinidadian guppies

Idealised models can provide useful insights into the inherent biases of AIs. However MLEs derived for the models may be difficult to apply to real studies. My model was motivated by the study on Trinidadian guppies described in the previous chapter and was developed to incorporate open populations in which animals may be outside the study area. In order to make an MLE calculable my model simplified the grouping behaviour of the animals. The model requires all groups to be the same size whereas group sizes in the guppy study ranged from singletons to a group of over 50 fish. The model also requires the number of groups observed (j) and the total number of groups in the pool (k) to be the same in each census. The number of guppy shoals caught varied between 20 and 43 per census and k was unknown for every census. In addition q was not known for the guppy study. As a result of these differences it is not only very difficult (or perhaps impossible) to calculate EB1 for the guppy study, but also the low bias benefits of using EB1 may not be realised when many of the assumptions are violated.

Cairns and Schwager (1987) acknowledges that CS1 is hard to use in practice and instead suggest that in each study assessment of bias in light of their simulation results should be used to choose between ratio indices. Here the results of my simulation can be used to inform a new AI which is less biased than conventional ratio indices and easier to calculate than EB1. Using the framework set out in Section 6.2 I can construct a *GI* by considering its constituents, *SF* and *LI*. A reasonable choice for an *SF* would be the probability that both animals are in the study area, which is equal to q^2 . I use ratio indices for *LI*, even though they are not strictly *LIs*.

After exploring a few ideas and noting that Figure 6.4c shows that HWI is less biased than SRI at high q and SRI is less biased than HWI at lower q , I found the best performing option to be a weighted sum of HWI and SRI. I shall refer to this new AI as the ‘q-weighted index’ (QWI) and it is defined as

$$\text{QWI} = q^2\text{HWI} + (1 - q^2)\text{SRI}. \quad (6.7)$$

The bias of QWI can be compared to that of HWI and SRI using the simulation described in the previous section. The bias as a function of parameters p , q and j/k is shown in Figure 6.5. QWI has a smaller bias than SRI and HWI across the full range of parameters.

To apply QWI to the guppy study a value needs to be found for q . This issue will be considered in the following section.

6.4.1 Estimating q

Since data were not collected with a view to measuring q , the actual value of q for each guppy is unknown. Instead, a sensible estimate of q must be obtained from the available data. There are not enough observations to be able to estimate q for each individual fish. However by combining observations for many fish, an estimate can instead be obtained for the average value of q for males and females separately. Figure 6.6 is a reminder of the distribution of recapture frequencies for males and females from the previous chapter. The distributions for the two sexes are clearly different which supports the idea of analysing them separately. A reasonable estimate of q for the guppy study is found by calculating the mean

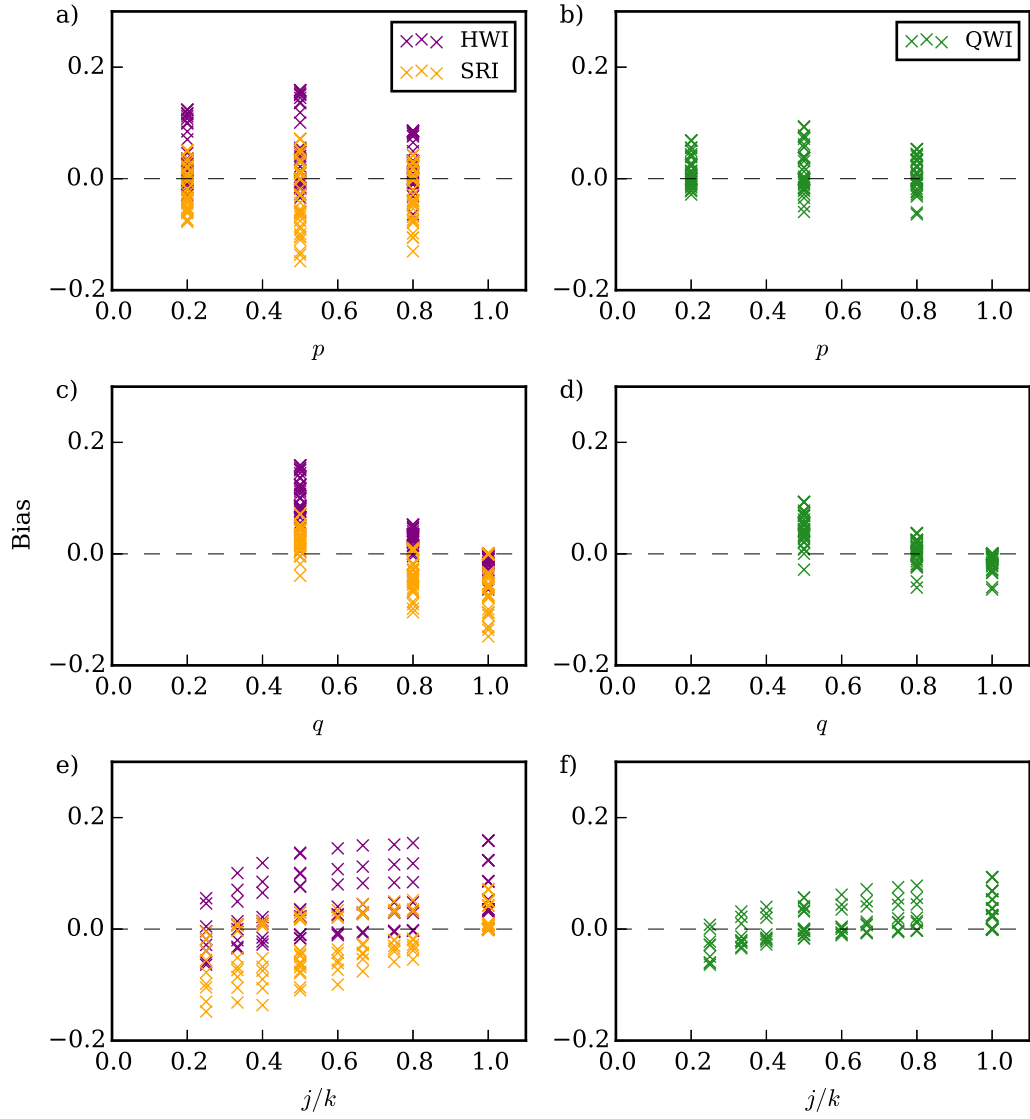


Figure 6.5: Variation of AI bias with parameters a) & b) p , c) & d) q and e) & f) j/k . a), c) & e) Comparison of HWI and SRI bias. b), d) & f) QWI bias.

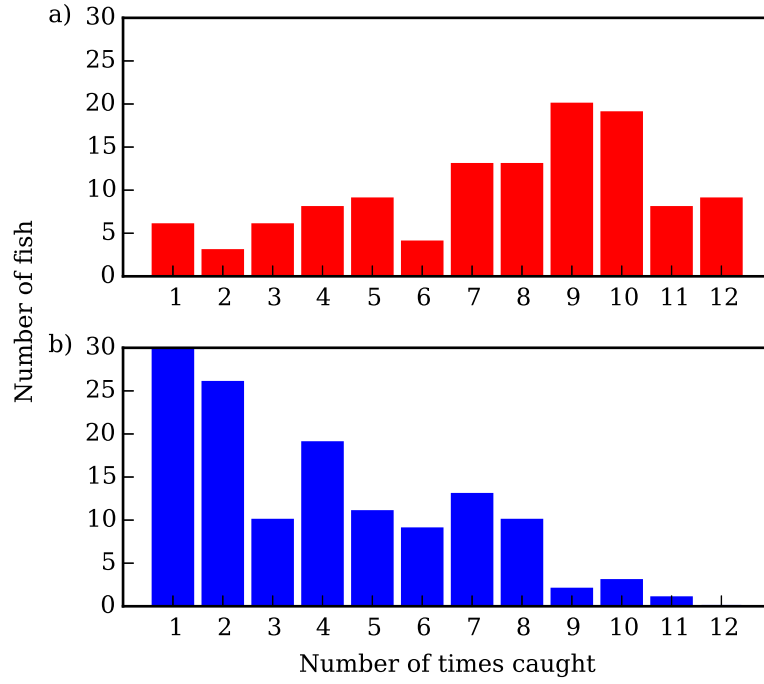


Figure 6.6: *Distribution of the number of times guppies were recaptured for a) females and b) males.*

fraction of censuses in which males and females are caught. This gives an estimate of $q_M = 0.33$ and $q_F = 0.62$ for males and females respectively. These values are underestimates as not all fish in the pool were observed in each census. However the number of unobserved fish is likely to be only a small percentage of the total as only singletons in the pool were not recorded (D.P. Croft, personal observation).

6.4.2 Comparison of HWI, SRI and QWI

Pairwise association strengths for the guppy dataset were calculated using HWI, SRI and QWI and networks were constructed using each of these indices. The overall network structure is the same for all three indices as edges exist between all pairs of fish which have been seen in the same shoal at least once. Edge weights however vary depending on which index is used.

One way of finding the most important or reliable structures in a network is to filter the edges to include only the top E edges when ranked by edge strength.

The rankings of edges can be dependent on the AI used therefore after filtering different edges may remain. To demonstrate the difference this can make I have chosen two filter levels and applied them to each of my three networks. As there were only 10 censuses in the guppy study many edges shared the same edge weights and when choosing how many edges to include it was therefore necessary to pick a number which did not separate edges with equal edge weights. It proved impossible to find a single number of edges which would not split equally weighted edges in both SRI and HWI so instead I have adjusted the included number of HWI edges to be as close as possible to the number for SRI.

Figure 6.7 shows the guppy network filtered with a medium filter (left hand column) and a strong filter (right hand column). SRI, QWI and HWI have been used to calculate association strengths for the networks on the top, middle and bottom rows respectively. The medium filtered networks contain either 84 (SRI and QWI) or 90 edges (HWI) and the strongly filtered networks contain either 31 (SRI and QWI) or 34 edges (HWI). Nodes are coloured according to guppy sex with red for females and blue for males. To de-clutter the layout only nodes which have at least one edge using any one AI (in each column separately) are included. In order to emphasise the differences between the networks the layouts have been kept the same in each column and isolates have been left white. Edge widths are proportional to association strength.

There are some striking differences in structure between the networks constructed with the different indices. For example in the medium filtered networks, the largest component in the QWI network is much larger than in the HWI network (38 and 17 nodes respectively) and is also larger than in the SRI network (31 nodes) (Fig. 6.7a, c & e). Many other structural differences can be seen including locations of connected triads and differences in degree sequence. The medium filtered HWI network contains two nodes with a degree of 5 whereas the highest degree for both the SRI and QWI networks is 4. This contributes to the higher mean degree of the HWI network (1.75 compared to 1.60 and 1.56 for QWI and SRI respectively). Comparing the positions of the white isolates in each network shows that the choice of index also influences which nodes are included in the network.

The choice of index also alters the relative strengths of FF and MM associations. Counting the numbers of FF and MM edges in the filtered networks reveals that

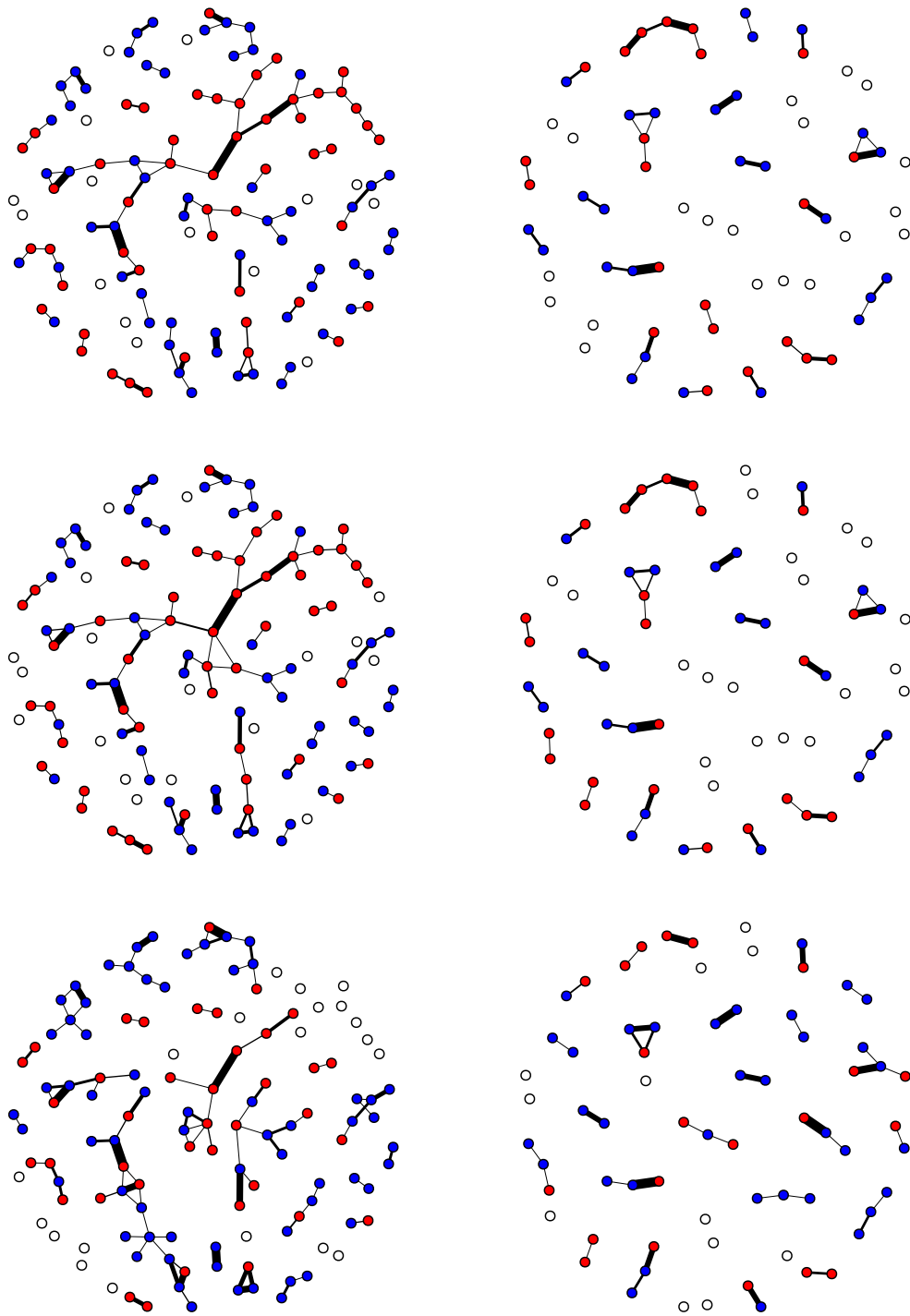


Figure 6.7: Social network of Trinidadian guppies using a) & b) SRI, c) & d) QWI and e) & f) HWI to calculate edge weights. A medium filter has been used for a), c) & e) including 84 edges for SRI and QWI and 90 for HWI. A strong filter has been used for b), d) & f) including 31 edges for SRI and QWI and 34 for HWI. Red nodes represent females and blue represent males. In each column the layouts have been kept the same and only nodes having at least one edge using any of the AIs are included. Isolates have been left white.

| | Medium filter | | | Strong filter | | |
|-------|---------------|------|------|---------------|------|------|
| | SRI | QWI | HWI | SRI | QWI | HWI |
| All | 84 | 84 | 90 | 31 | 31 | 34 |
| FF | 28 | 30 | 14 | 9 | 10 | 4 |
| MM | 28 | 27 | 41 | 11 | 10 | 16 |
| MF | 28 | 27 | 35 | 11 | 11 | 14 |
| FF/MM | 1.00 | 1.11 | 0.34 | 0.82 | 1.00 | 0.25 |

Table 6.9: *Breakdown of numbers of edges in each network.*

SRI contains far more FF edges compared to MM than HWI (Table 6.9). When using QWI the proportion of FF edges as compared with MM edges even greater than when using SRI. This result is seen at both filter levels.

6.5 Discussion

In this chapter I have considered the difficulty of finding an appropriate AI for open populations where animals can move outside the study area. This research has been motivated by the Trinidadian guppy study described in the previous chapter.

Previous studies on the Trinidadian guppy have used either SRI (Croft et al. 2009b) or X (Croft et al. 2004a, Croft et al. 2005, Croft et al. 2006) to quantify association strength. The purpose of Section 5.7 was to search for a correlation between two relational variables, the pairwise association strengths and the relatedness values. Initially the SRI was tried as the AI but it was found that both the SRI and the relatedness values had too many tied values for a correlation statistic to be meaningful. There was also not enough variation in X to enable a correlation with relatedness. Instead a filter of $X \geq 2$ was used to select only pairs of fish having repeated associations and the frequency of relatedness values of the selected pairs were analysed. The decision not to use SRI for the analysis does not mean that SRI would not be an appropriate index for other guppy studies or that it would not be appropriate for this study had a different research

question been asked.

Following Cairns & Schwager's recommendation I derived an MLE, EB1, for an idealised model of the guppy study. Using Cairns & Schwager's Model 1 as a starting point I extended this to incorporate open populations. Simulated observation data showed EB1 to be less biased than SRI, HWI and CS1 over all parameter combinations and to have similar variance. In order to calculate EB1, values for k (the number of groups in the study area) and q (the probability of an animal being inside the study area) need to be found. Neither of these values can be calculated from observations of group membership and therefore it would not be practical to apply EB1 to a real study.

In order to address this problem I constructed QWI as an AI (which is not an MLE) which in practice is easier to calculate. Tests of QWI on my simulated model data showed it to be less biased than HWI, SRI and CS1 and as expected more biased than EB1. Estimation of q for male and female guppies allowed QWI to be calculated for the Trinidadian guppy study. Alternatives to this method of estimation may be found in mark-recapture method literature in which maximum-likelihood methods are used to estimate the probability of recapture when there is immigration and emigration from the study area (Pollock 1982, Whitehead 1990). It is possible these could be adapted to yield estimates for q .

Comparison of HWI, SRI and QWI using the Trinidadian guppy dataset revealed that when filtering to retain the strongest edges, network structure is largely dependent on the choice of AI. Network structure is assessed at this stage and if it does not accurately portray the social structure then interesting biology may be overlooked or false conclusions drawn. When classifying nodes according to sex it was found that more than twice as many FF edges were retained when using SRI and QWI than when using HWI. Such large differences between resultant networks means that the choice of AI may affect the conclusions of studies.

In the relatedness analyses of the previous chapter (Sec. 5.7) the AI, X , was only used to filter out associations where a pair had only been found in the same group once and was not used subsequently to differentiate the association strengths of the surviving edges. It remains a sensible step to use X to eliminate non-repeated associations from the analyses as repeated associations are more likely to provide evidence for social preferences. Since the remainder of the analyses

did not differentiate edges by association strength but instead by relatedness, the conclusions of these analyses are unaffected by the work in this chapter.

For the colour analyses also in the previous chapter (Sec. 5.8) edge weights, computed using X , were used to calculate the test statistic and so using a different AI has the potential to alter the conclusion. Since the colour analysis involved only MM edges and a single q_{MM} has been estimated for all MM edges, performing the analysis using QWI instead of X may not have a large effect. Nevertheless it is impossible to predict whether using QWI would change the conclusions and so I repeated the randomisation tests of Section 5.8.2 using edge weights calculated with QWI. I found that the test percentiles using QWI were similar but not identical to the test percentiles using X . The two colour attributes for which significant test statistics were found had test percentiles of 0.81 and 1.10 (TC) and 2.04 and 2.60 (PC) for X and QWI respectively, which are all below the 5% significance level. Therefore in this analysis using QWI did not change the outcome of the hypothesis tests however the possibility still remains for other studies.

It is impossible to assess the bias of indices on the guppy dataset as the actual association strengths are not known. As a result it is not possible to be sure which of the indices gives the most accurate estimates of association strength. For this reason a model where the true association strengths are known can be a useful tool for comparison of indices. Results obtained from a model should be treated with caution as it is not necessarily true that the best performing AI for the model will perform the best for a real study. However models are a useful starting point and with careful construction can be tailored to explore the effects of biases which may be present in real studies.

Selecting an appropriate AI remains a difficult problem and the choice should be considered carefully for each new study. The work in this chapter contributes a piece to the puzzle with many pieces still to be found.

Part III

Analysis of automated temporal data

Chapter 7

Potential for social learning in a population of New Caledonian crows (*Corvus moneduloides*)

The analysis in this chapter was carried out in collaboration with C. Rutz and co-workers and contributes to ongoing research into the New Caledonian (NC) crow (*Corvus moneduloides*). The work herein contributes to St Clair et al. (in prep.) and uses data collected in October 2011 from a population of wild NC crows. The experiment was conceived by C. Rutz and fieldwork was led by C. Rutz, J. St Clair and Z. Burns. The Encounternet technology which facilitated this study was developed by J. Burt and B. Otis. Genetics analysis was carried out by T. Ryder and R. Fleischer.

7.1 Introduction

NC crows, endemic to New Caledonia, have remarkable tool using and tool making abilities (Holzhaidner et al. 2011). Part of the Corvid family, of which many members are well known for their intelligence (Emery 2004), NC crows display the most advanced tool making abilities of all non-human animals (Hunt 1996).

Tool use was first discovered in non-humans by Jane Goodall in 1960 when she

observed chimpanzees using twigs to fish for termites in the ground (Goodall 1964). Since then tool use has been observed in an increasing number of species from many parts of the animal kingdom including non-primate mammals, invertebrates, amphibians, reptiles and birds (Shumaker et al. 2011). There is however wide variation in the complexity of tool use (Rutz and St Clair 2012). NC crows have relatively sophisticated skills and in addition manufacture tools which is far rarer (Hunt and Gray 2003). This makes NC crows an interesting species to study as behavioural ecologists attempt to gain insight into the evolution and maintenance of tool use (Rutz and St Clair 2012).

Tools are used by NC crows as a way to forage for food (Hunt 1996) (Fig. 7.1). Wood-boring longhorn beetle larvae (*Agrianome fairmairei*) live in burrows inside candlenut trees (*Aleurites moluccana*) and these are a protein and lipid rich food source for the crows (Rutz et al. 2010). Crows obtain larvae by inserting tools into burrows teasing the larvae with repeated poking (Rutz et al. 2010). The larvae then bite the tool with their mandibles and can be pulled out by the crow (Rutz et al. 2010).

NC crows manufacture two types of tools, those made from twigs and those made from Pandanus leaves (*Pandanus* sp.) (Hunt 1996) (Fig. 7.1d). Tools made from twigs are stripped of leaves and bark and may be fashioned to have a hook at one end (Hunt and Gray 2004). Tools made from Pandanus leaves take advantage of the barbs occurring on the edges of the leaves (Holzhaidner et al. 2010). Long thin strips are cut from the edges of the leaves to create a tool with barbs along one edge. Three different types of Pandanus leaf tool exist, uniformly narrow, uniformly wide, and stepped tools which are wide at the end held in the beak and narrow at the other end (Hunt and Gray 2003). The manufacture of all types of tools requires a process of several steps and for stepped Pandanus tools it is only after the final cut which separates the tool from the leaf that the tool becomes functional (Holzhaidner et al. 2010). It is therefore thought that the design of the tool must be determined before the start of manufacture (Holzhaidner et al. 2010).

Hunt (2000b) documented the shapes and locations of tools found in New Caledonia and found differing geographical distributions of the three Pandanus tool designs which did not correlate with any obvious ecological differences between the locations. These findings led Hunt to suggest that the diversification of Pandanus tool designs was brought about by a process of cumulative technological



Figure 7.1: a) & b) NC crow using a tool to forage for beetle larvae inside a candlenut tree. c) Cross-section of a longhorn beetle larva in a burrow in a candlenut tree. d) Range of different tools made from sticks and *Pandanus* leaves used by crows to dig inside burrows. Photos reproduced from Rutz and St Clair (2012) a) & b) J. Troscianko, c) J. St Clair d) C. Rutz and J. St Clair.

evolution and could be mediated by social learning.

Several factors have been proposed to explain the drivers of tool use in NC crows. Firstly the abundance of concealed food and the lack of competitors with the ability to extract it (for example woodpeckers (*Picinae* sf.), chimpanzees (*Pan troglodytes*) or aye-ayes (*Daubentonia madagascariensis*)). Together with low or seasonal availability of other food sources this would make tool use more profitable relative to conventional foraging behaviours and so promote selection for tool use (Rutz and St Clair 2012). There is also low predation risk for NC crows (one predator being the goshawk (*Accipiter* sp.) (Holzhaidner et al. 2011)). This lack of predators means that NC crows can devote more of their attention to problem solving instead of being watchful for predators (Rutz and St Clair 2012).

Several studies have begun to address the question of how NC crows may have evolved the use of tools. Kenward et al. (2005) reported a lab based experiment using four NC crows bred in captivity and found evidence that tool making skills

are at least partly inherited. The four crows were reared without ever observing an adult crow. Two of the four crows were given demonstrations by humans on how to use twigs to retrieve food while the remaining two never saw tool use. All four crows were raised in an aviary which contained an assortment of twigs and also hidden food items in holes. After around 2–3 months all four crows successfully managed to retrieve hidden food items using twigs. The birds were later presented with Pandanus leaves and one bird successfully managed to cut a tool from a leaf and use it to remove food from a crevice. Although this study shows that the ability to manufacture and use tools is at least partly inherited, the tools made by the study birds did not resemble the tools made by crows in the wild and so it is possible that social input may be required for honing techniques.

The opportunity for social learning may be gauged in part by determining the social structure of NC crow societies. NC crows live in dense forest and are sensitive to human disturbance so observations of social associations between crows have so far been limited (Rutz et al. 2007). Preliminary observations of sociality were made by Hunt (2000a) and Kenward et al. (2004). Hunt (2000a) observed ~ 30 crows in a tree which he suggested was a temporary aggregation of small groups. Kenward et al. (2004) observed crows flying above the canopy and saw groups of crows ranging from 2–8 members with a median and mode of 3. The groups appeared fluid with birds leaving and joining groups. They also observed ‘juvenile begging behaviour and feeding by regurgitation’ which strengthens the view that social groups are family groups.

Holzhaider et al. (2011) conducted a study aimed at gaining further knowledge of the social structure of NC crows. The main part of the study focussed on observing birds at a feeding station. Initially 28 individuals were caught, tagged and assigned to family groups. Adult crows were assumed to be partners if they were observed engaging in courtship, feeding or nesting together or feeding the same juvenile. Parent offspring relationships were identified by observing parental feeding, intensive begging or prolonged periods of a juvenile following an adult. Holzhaider et al. (2011) found that whilst there were occurrences of males tolerating non-family members at feeding stations, it was common for a non-family juvenile to stop feeding and act submissively while a male from another family was present.

Holzhaider et al. (2011) also undertook tracking of birds using bird mounted

radio-transmitters (made by Sirtrack Ltd). A single crow would be followed over a period of several hours and the presence of any nearby crows was recorded. This process was hindered by the dense forest conditions making it difficult to stay in visual contact with the birds. In accordance with observations at feeding tables, radio-tracked crows were mostly observed foraging in family groups. There were also a few occurrences of non-family crows being close to radio-tracked crows however this was generally not during foraging periods. Through assessment of the social associations of crows, Holzhaider et al. (2011) concluded that the potential for transmission of tool skills is far greater vertically (from parent to offspring) than horizontally or socially (between non-family members).

The study here aims to further assay the potential for social transmission of tool use and tool manufacture behaviour by providing a more detailed picture of crows' social associations. This study uses a system of miniature bird mounted proximity loggers (Encounternet) which record all instances of crows coming within tens of metres of each other. Encounternet (developed by J. Burt, B. Otis and J. Bowen from the Department of Electrical Engineering, University of Washington) is a relatively new technology with the first field test reported in Mennill et al. (2012). The small size of these tags (~ 10 g) has enabled biologists to begin to employ them for social studies of birds (St Clair et al. in prep.). The study here is the first to analyse data streams arising from bird to bird proximities (as opposed to bird to fixed basestation) and this brings with it new challenges (Sec. 7.3). Methods of processing and analysing these data are considered here for the first time.

Encounternet logs the start time, duration and signal strengths (indicating proximity) of all crow to crow *encounters* enabling a complete record of crow associations between all birds over the duration of the study. Encounternet allows for a far richer data set of social interactions than has previously been obtained as it overcomes the difficulties of observing NC crows in their natural habitat (Rutz et al. 2012). Encounters could be filtered to include only close range encounters (≤ 5 m) where it is more likely that crows would be in visual contact and hence the opportunity for social learning could arise (St Clair et al. in prep.). In addition to collecting timestamped proximity data, crows were also genotyped allowing family groups to be distinguished and hence the potential for inter-family transmission of skills to be assessed.

Two types of network analysis will be used to analyse this timestamped dataset. Firstly static social networks will be constructed by aggregating encounters over a specified time period and weighting edges by total duration or some function of proximity. This can provide a good basic understanding of the relative association strengths between all crows. The second analysis method is to consider the full temporal network of encounters. As described in Section 2.3, edges in temporal networks are transient and have a defined start and end time. In this study I build a temporal network in which edges are logged encounters between crows.

Having a temporal network of crows' encounters enables more detailed analysis of the potential for social transmission of information. Using a simple Susceptible-Infected (SI) algorithm, common in epidemiology (Hamer 1906), I have emulated the spreading of information through the temporal network. This was done by supposing one crow to have knowledge of some new innovation at the beginning of the day. Assuming that knowledge of the innovation will be passed from an informed to an uninformed crow during an encounter between them the spread of the knowledge can be emulated by tracing information pathways through the temporal network. By running many emulations starting with different crows and on different days the potential for information flow through the network can be assessed.

Whilst other ASN studies have analysed the flow of information (or disease) through the network, most play out an SI or related model on a static network (e.g. Aplin et al. 2012, Allen et al. 2013). One exception is Hamede et al. (2012) where the underlying network was rewired at periodic intervals (see Sec. 7.6). Some studies, such as Naug (2008) (honeybees) and Sendova-Franks et al. (2010) (rock ants), were fortunate enough to have been able to gather data on real transmission pathways but in these cases it was facilitated by being able to video record the population. In the absence of real transmission pathways, this study has instead used emulations to consider which transmission pathways are possible. This is to our knowledge the first study which has implemented an SI model on a temporal animal network.

The work in this chapter is organised as follows. First I describe how the Encounternet system was deployed and give details of how the study was carried out. I then describe the process of converting information from Encounternet log files into symmetrical temporal network data. The main section of work in-

volves analysing the results of emulations played out on the temporal network. Throughout the chapter emphasis is also placed on finding effective visualisations to display both the temporal network and emulation results.

7.2 Study details

7.2.1 Overview of Encounternet system

The Encounternet system used in this study consists of bird-mounted transceiver tags and a grid of fixed *basestations* throughout the study site. Each transceiver tag emits pulses which broadcast a unique ID code at a user-defined frequency. The tags also continually listen for signals. When two tags come within range of each other (several tens of metres) each tag opens a log file which records data about the *encounter* – the received ID code, the start and end times of the encounter and a measure of signal strength. During an encounter the signal strength is recorded as a ‘received signal strength indicator’ (RSSI) value which is a measure of the power ratio (in dB) of the received signal referenced to one milliwatt (Rutz et al. 2012 suppl.). The RSSI value is converted to an integer by the electronics and will henceforth be unitless. At the end of each encounter RSSI values received are summarised as the minimum, maximum and mean RSSI (RSSI_{\min} , RSSI_{\max} and $\text{RSSI}_{\text{mean}}$) values which are recorded. The proximity of the tags can later be estimated from the RSSI values since the signal strength attenuates with distance (St Clair et al. in prep.). Other factors affect the RSSI values apart from distance for example habitat and the relative orientation of the two birds during the encounter so the calibration of RSSI to distance is not exact and averages over these other factors (Burns et al. in prep.).

In contrast to the bird-mounted tags, the basestations operate only in ‘receiver’ mode. Basestations continually listen for signals so that when a tag comes within range of a basestation, the basestation will record a log of the presence of the tag in the same way that tag to tag encounters are recorded. In addition, when near a basestation tags download all their log files to the basestation for storage. An advantage of having a grid of basestations is that locations of birds can later be estimated through a process of cross-triangulation.



Figure 7.2: *a) A tagged crow wearing a harness mounted transceiver. b) Basestation hanging in a tree. Photos by J. St Clair reproduced from Rutz et al. (2012).*

At night time, so as not to disturb the birds, researchers use *masternodes* to download data wirelessly from basestations or tags. Masternodes are hand held Yagi antennae which the researcher can carry through the study area collecting data from nearby basestations or tags.

7.2.2 Experimental setup

In this section I provide an overview of the experimental setup and technical details used in this study. Since I was not involved in the data collection or planning of the experiment I present here information necessary for understanding this study and details relevant to my analysis. A complete account of the experiment is provided in the supplementary material of Rutz et al. (2012).

The study was based in the Taro and Tabou valleys of Gouaro-Dèva (21°40'S, 165°19'E) on the central west coast of Grande Terre, New Caledonia. Meat-baited whoosh nets (Kenward et al. 2004) were used to trap crows at four different trapping sites between the 2nd and 21st October 2011 (Fig. 7.3). A total of 41 crows were captured of which 33 were eventually used for the study. Trapped birds were sexed using molecular techniques and age was inferred from gape colouration (the interior of the mouth). Gape colour changes from pink to black during the first few years of life and so ages were categorised as juvenile (pink gape), immature (grey gape) or adult (black gape) (Rutz et al. 2010). Tags were

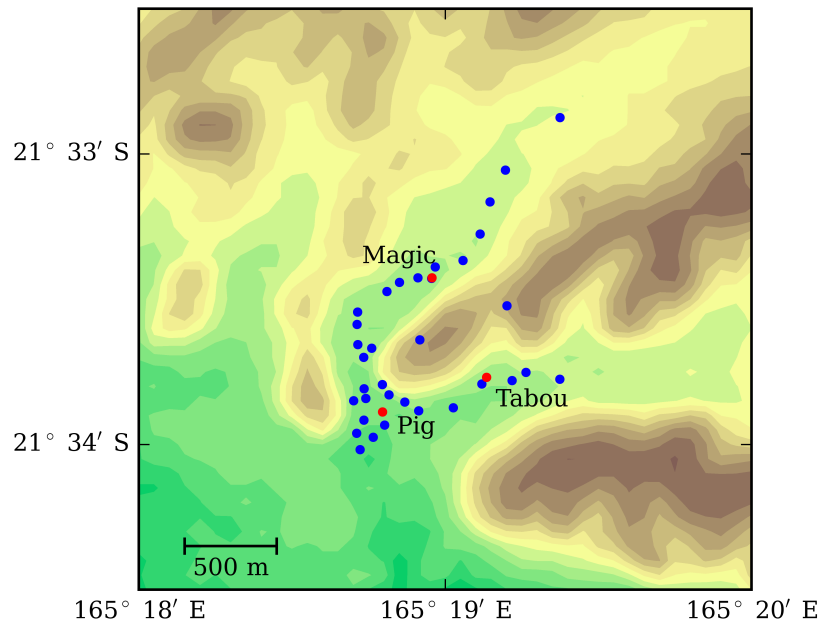


Figure 7.3: Map of the study area on the west coast of Grande Terre, New Caledonia. The crows used for the study were captured near to trapping sites Magic, Pig and Tabou, shown by red circles. The positions of the fixed basestations are indicated by blue circles.

attached to crows using weak-link harnesses which gradually degraded to release the harness and tag after several months. The 33 crows used for the study were captured from 3 of the 4 trapping sites, Magic (20 crows), Pig (12 crows) and Tabou (1 crow) (Fig. 7.3). The 33 crows consisted of 19 males and 14 females of which 22 were adults, 6 immatures and 5 juveniles. The attributes of all crows are shown in Table 7.2 and summarised in Table 7.1.

45 basestations were deployed in the study area along the creeks of two convergent valleys (Fig. 7.3). Basestations were mounted in the crowns of tall trees and as far as possible away from foliage and large branches (Fig. 7.2). Obstructions such as foliage increased signal attenuation and so avoiding these as much as possible increased the range at which basestations could detect signals emitted by tags.

7.2.3 Experimental timeline

Tags were programmed to switch on 5 full days after trapping on 27th October 2011. This waiting period was intended to allow the behaviour of the crows to return to normal after the disturbance of trapping. The study took place over

| Capture site | Sex | Age category | Num crows |
|--------------|--------|--------------|-----------|
| Magic | Female | Adult | 4 |
| | | Immature | 2 |
| | | Juvenile | 2 |
| | Male | Adult | 9 |
| | | Immature | 1 |
| | | Juvenile | 2 |
| Pig | Female | Adult | 3 |
| | | Immature | 1 |
| | | Juvenile | 1 |
| | Male | Adult | 5 |
| | | Immature | 2 |
| Tabou | Female | Adult | 1 |

Table 7.1: *Summary of crows used in the study.*

19 days in total, the duration being limited mainly by the battery life of the tags. Tags were programmed to be active between 4:00–20:00 hrs each day which comfortably included all daylight hours.

The duration of the study allowed time to perform a manipulation on the system. Manipulations are rare in ASN studies (a notable example is Flack et al. 2005) and even rarer is the opportunity to perform manipulations on animals in the wild (Pinter-Wollman et al. 2014). However manipulations provide the chance to scrutinise a hypothesis by analysing the effect of controlled perturbations on the system (Rands 2014). Here the study follows a ‘baseline-manipulation-return to baseline’ paradigm. During the manipulation period, the availability of food was increased to see if this affected the network structure and consequently the potential flow of information through the network.

For the seven days following the 27th October, the system was observed in the absence of any external influences in order to establish the nature of the crow network. This period will be referred to as the baseline (B). During this period time aggregated networks were constructed each night and network measures calculated in order to view the accumulation of the network over the seven day period.

Following the baseline period, experiment 1 (E1) was performed during days 8–10. After nightfall on day 7, a tree-fall event was simulated by placing a section

| Tag ID | Sex | Age category | Capture site |
|--------|-----|--------------|--------------|
| 10 | M | I | M |
| 11 | F | J | M |
| 19 | F | I | M |
| 22 | M | A | M |
| 29 | M | A | P |
| 32 | F | J | M |
| 35 | M | A | M |
| 38 | M | J | M |
| 40 | F | A | M |
| 42 | M | A | M |
| 47 | F | I | M |
| 49 | F | A | M |
| 54 | M | J | M |
| 56 | M | A | M |
| 58 | F | A | M |
| 59 | M | A | M |
| 61 | M | A | M |
| 66 | M | A | P |
| 67 | M | A | M |
| 68 | M | A | P |
| 71 | M | A | M |
| 72 | F | J | P |
| 73 | M | I | P |
| 74 | F | I | P |
| 75 | F | A | P |
| 76 | M | I | P |
| 77 | M | A | M |
| 78 | F | A | M |
| 79 | M | A | P |
| 80 | F | A | P |
| 81 | F | A | P |
| 84 | M | A | P |
| 85 | F | A | T |

Table 7.2: *Attributes of the 33 crows used in this study. Key: Sex: M : Male, F : Female; Age category: A : Adult, J : Juvenile, I : Immature; Capture site: M : Magic, P : Pig, T : Tabou.*

of candlenut tree midway between capture sites Magic and Pig in the centre of the study site (Fig. 7.3). Burrows in the tree section were implanted with beetle larvae mimicking the natural plentiful food sources that occur when trees fall. Monitoring the network topology during the collection of the data showed that no significant changes in the network were induced during days 8–10 and so E1 was aborted. After nightfall on day 10, the original candlenut tree section was removed from the study area and two further candlenut tree sections were introduced this time at the centre of Magic and the centre of Pig (Fig. 7.3). This commenced the period experiment 2 (E2) which ran during days 11–14. Monitoring of data during this period revealed a large increase in activity and so there was sufficient confidence that the network would show an effect from E2.

At the end of day 14 the two introduced candlenut tree sections were removed and encounters were recorded for a further 5 days (days 15–19) in a ‘return to baseline’ (RB) period. The aim in this period was to observe the network return to its initial baseline state.

7.2.4 Inferring encounters from logged signals

Tags were programmed to emit pulses with a period of 20 s. This period was chosen to be significantly less than the expected time-scales on which crow fission-fusion events happen (minutes to tens of minutes) to enable resolution of all encounters (Rutz et al. 2012). Tags are unable to receive signals during the brief periods when they are transmitting and so the transmission times were set at random on each tag in order to minimise missed pulses.

Each time two crows come within range of one another, two log files will be recorded, one by each of the crows’ tags. These will be referred to as *reciprocal encounters*. An example of the timings of pulses transmitted and received by two tags during and either side of an encounter is shown in Figure 7.4a. This figure is intended solely to demonstrate the timings of the pulses while ignoring the signal strength. As such the y-axis has no scale. Figure 7.4b shows how the encounter would be logged by each tag. Without knowledge of the timings of pulses, the encounter would be reconstructed from the log file as shown in Figure 7.4c. The figure demonstrates how the difference in transmission times of the two tags can cause a disparity in the start and end times of the encounter as recorded by each

tag. The differences in start and end times however should not be more than 20 s (the period of the pulses) and since the majority of encounters last at least 5 minutes (see Sec. 7.3) this does not significantly affect the study.

In order to run analyses on the data reciprocal encounters must be combined to produce a single record of each encounter. This process will be called *amalgamation* and will be described in Section 7.3.1.

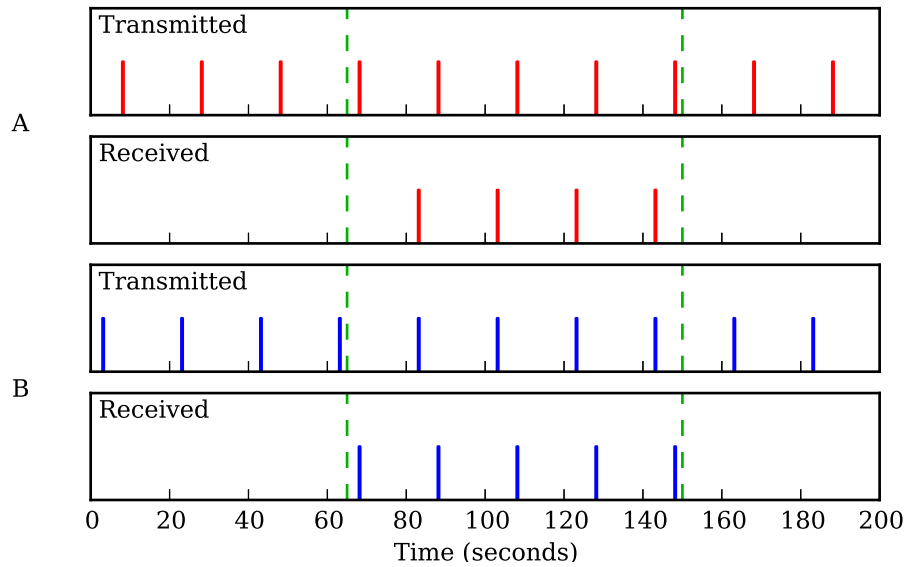
7.3 Preliminary data processing and analysis

Data recorded from the 19 study days amounted to just under 240,000 logs with all 33 crows participating in at least one encounter. The study was restricted to daylight hours in order to avoid encounters caused by roosting. Daylight hours were between 5:14–18:03 hrs on the first day of the study and increased to between 5:04–18:13 hrs on the final study day. Restricting to encounters between these hours reduced the number of logs to $\sim 177,000$.

Recorded signal strengths varied from -61 to 60 corresponding to distances of over 50 m to within 1 m. The distribution of $\text{RSSI}_{\text{mean}}$ values for all encounters is shown in Figure 7.5a. The sharp peak at $\text{RSSI}_{\text{mean}}$ was caused by a software error on the tags.

The distribution of encounter durations is shown in Figure 7.5b. The peaks at multiples of 20 s are a result of the tags emitting a pulse every 20 s (see Fig. 7.4). Tags were programmed to limit log files to a maximum of 300 s (5 min). In reality firmware bugs caused some logs to exceed this limit (as can be seen in Fig. 7.5b) and the maximum recorded log duration was 452 s (Rutz et al. 2012). If two crows remained within range of each other longer than 300 s then successive log files were created.

To give an idea of what the encounters between pairs of crows look like during one day the signal strengths of two pairs of reciprocal encounters are illustrated in Figure 7.6. These show the range of signal strengths (RSSI_{min} to RSSI_{max}) which occur in each encounter and also the mean signal strength ($\text{RSSI}_{\text{mean}}$) for each encounter. The plots show the variation in signal strengths from one encounter



| Transmitter ID | Receiver ID | Start | End | Duration |
|----------------|-------------|-------|-----|----------|
| <i>A</i> | <i>B</i> | 83 | 143 | 60 |
| <i>B</i> | <i>A</i> | 68 | 168 | 100 |

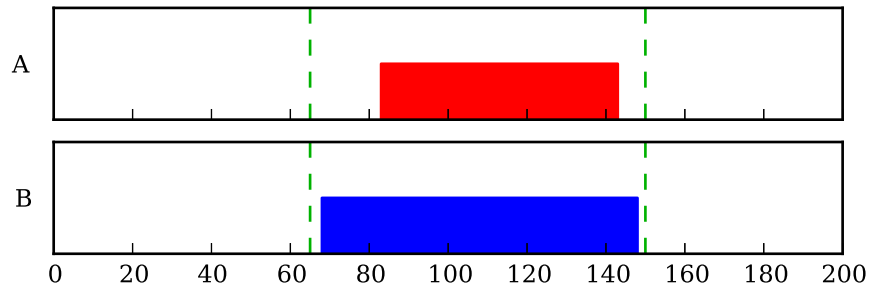


Figure 7.4: *Demonstration of how encounters are inferred from transceiver pulses. In this example it is supposed that crows A and B are within range of each other between $t = 65$ s and $t = 150$ s, indicated by the green dashed lines in (a) and (c). (a) shows the times at which signals are transmitted and received by A (top two plots) and B (lower two plots). (b) shows how the received signals are recorded in two lines of a log file. (c) shows how the encounter between A and B can be reconstructed from the log file. The upper plot shows the encounter according to what crow A received and the lower plot according to what crow B received. The disparity in start and end times for the encounter as perceived by A and B arises from the difference in times at which A and B transmit signals.*

to the next and also show that reciprocal encounters do not match exactly either in timing or in signal strength. This figure also illustrates how the majority of encounters appear to be the same length (~ 300 s) and successive encounters are separated by a small gap. The gap of around 20 s is another consequence of tags emitting a pulse every 20 s.

7.3.1 Filtering and amalgamation of reciprocal encounters

Spatial proximity is a symmetric proxy for association; if crow A is 10 m from crow B, then crow B is also 10 m from crow A. However the logs recorded by the tags are not perfectly symmetrical and this is due to two reasons. Firstly the sensitivities of tags are not identical and so there is variation in the RSSI values logged for the same distance. Independent calibration of tag sensitivities was not performed prior to the study and this would be highly recommended for any future studies. Secondly the immediate environment of the crows plays a part in attenuating signals and this can happen asymmetrically to the signals emitted by a pair of tags. More details of the factors influencing signal strength can be found in Burns et al. (in prep.), here I concentrate on the steps taken to clean the data as opposed to the cause of the discrepancies.

Figure 7.7 compares the recorded $\text{RSSI}_{\text{mean}}$ values for reciprocal encounters. Each plot shows the signals received by each tag of a pair plotted in red or blue. The shading has been made transparent so that the strengths of the reciprocal encounters are always visible. The five examples show a range of ways in which reciprocal signals can differ. The first type of discrepancy is that one tag in a pair can consistently record a higher signal strength than the other (Fig. 7.7a and e). Secondly in addition to this, all five examples show how the start and end times of encounters can differ. In some instances it is not even possible to match up pairs of encounters between the tags. Differences in encounter duration can be seen most easily in Figure 7.7e between 9:00–10:00 hrs where tag 74 (blue) records encounters with much shorter duration than tag 81 (red). Lastly Figures 7.7b and c show two pairs of reciprocal encounters both involving crow 72 (blue in both plots). Here it can be seen that tag 72 had an intermittent failure in the later half of the morning.

In order to build a symmetric network from the data, reciprocal signals must

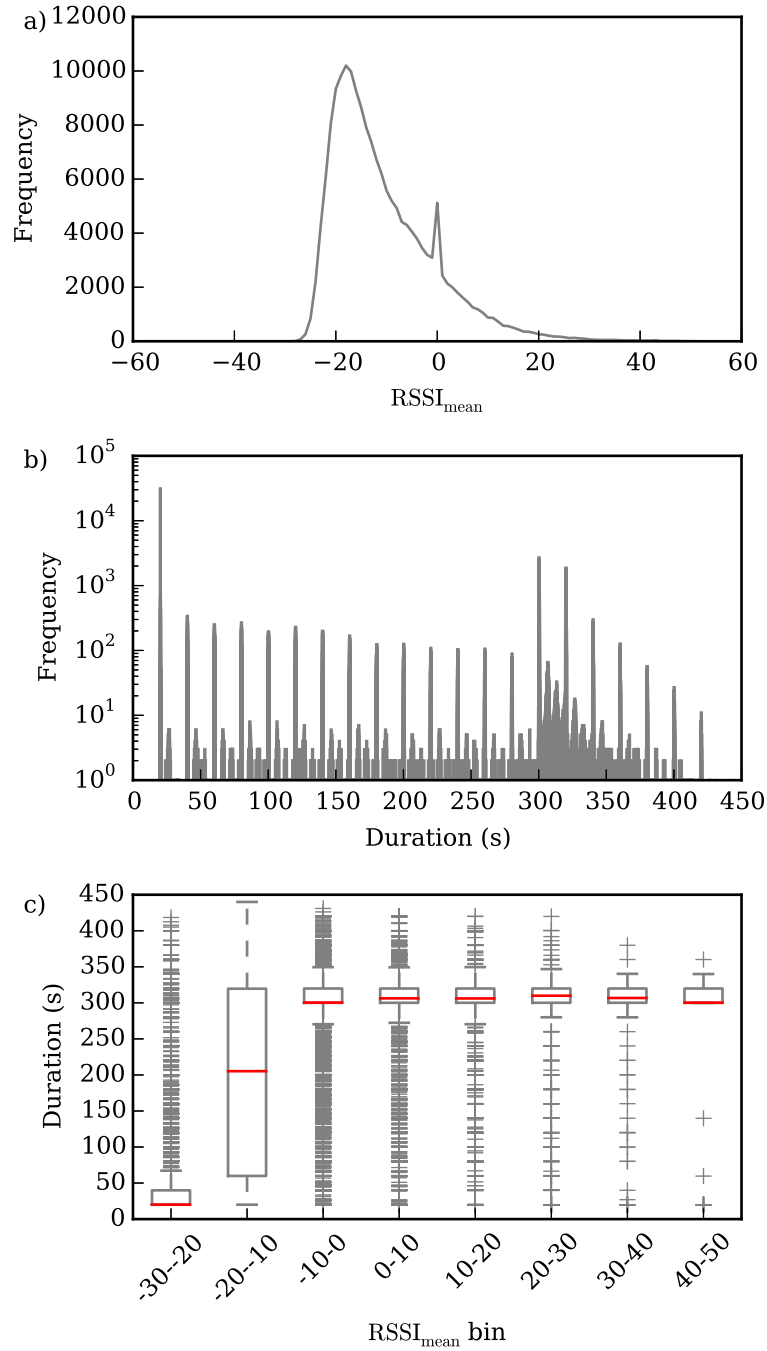
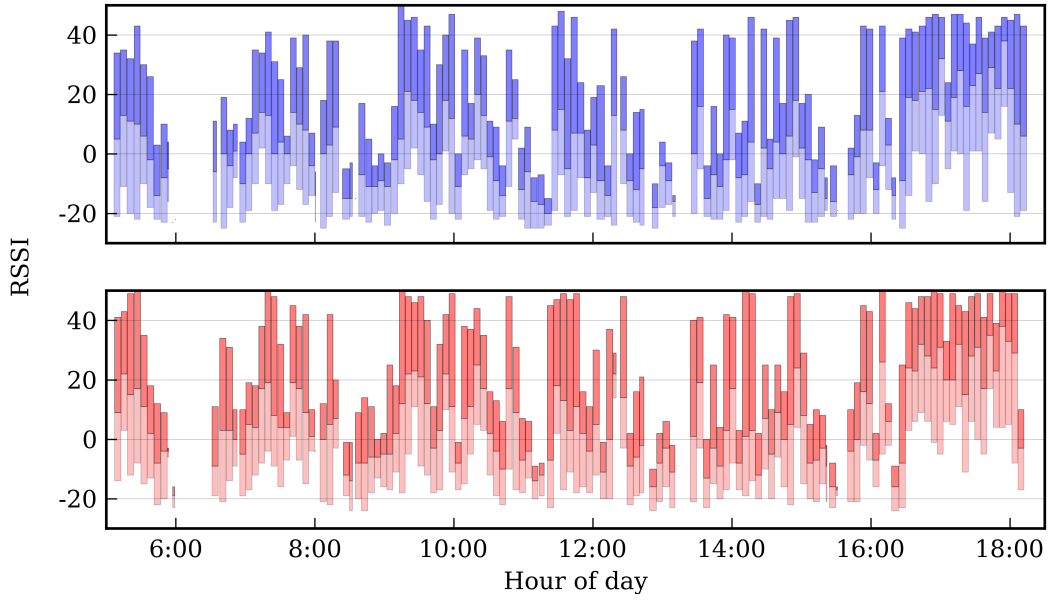
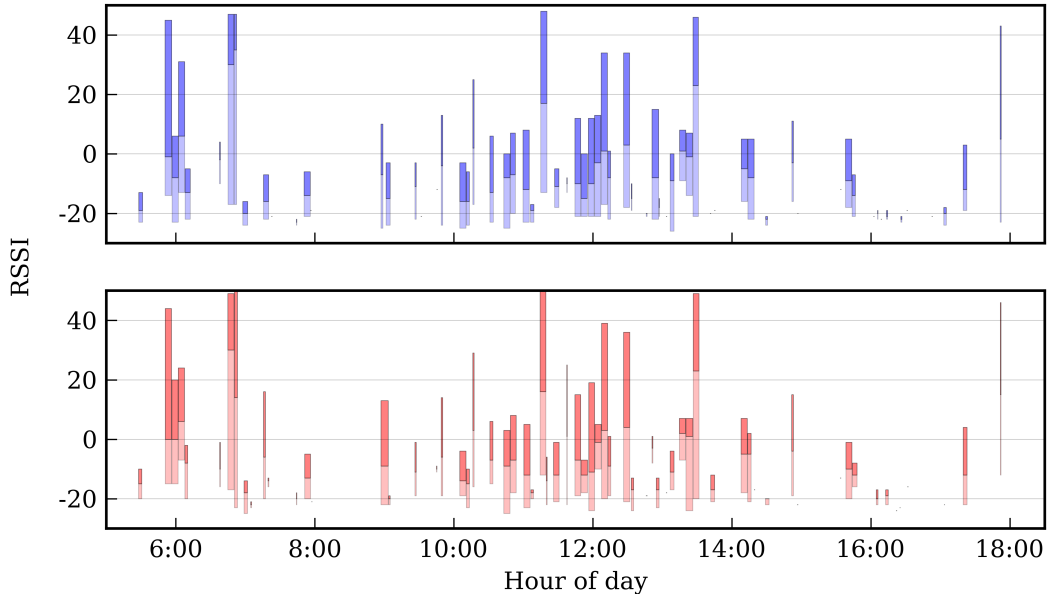


Figure 7.5: Properties of recorded encounters. a) Distribution of $RSSI_{mean}$ values for all encounters. b) Distribution of encounter durations for all encounters over all study days. c) Durations of encounters within different $RSSI_{mean}$ ranges. Boxes extend from the 25th to 75th percentiles, whiskers extend to the 2.5th and 97.5th percentiles and the median value is indicated by a red line. This shows that the distribution of durations is similar for all $RSSI_{mean}$ values -10–50 whereas encounters with $RSSI_{mean} < -10$ tend to have much shorter durations.



Encounters on day 15 between crows 74 and 81 as recorded by tag 74 (blue) and tag 81 (red).



Encounters on day 2 between crows 84 and 85 as recorded by tag 84 (blue) and tag 85 (red).

Figure 7.6: Two examples of reciprocal pairs of encounters over a day. Each encounter is shown as a shaded bar (blue or red) extending vertically from the minimum to the maximum RSSI values recorded during the encounter and horizontally from the start to end time of the encounter. Between $RSSI_{min}$ and $RSSI_{mean}$ the bars are shaded in light blue or red and from $RSSI_{mean}$ to the $RSSI_{max}$ the bars are shaded in a darker blue or red. a) and b) show the contrast in encounter patterns between two different pairs of crows with crows 74 and 81 (a) associating more frequently than crows 84 and 85 (b).

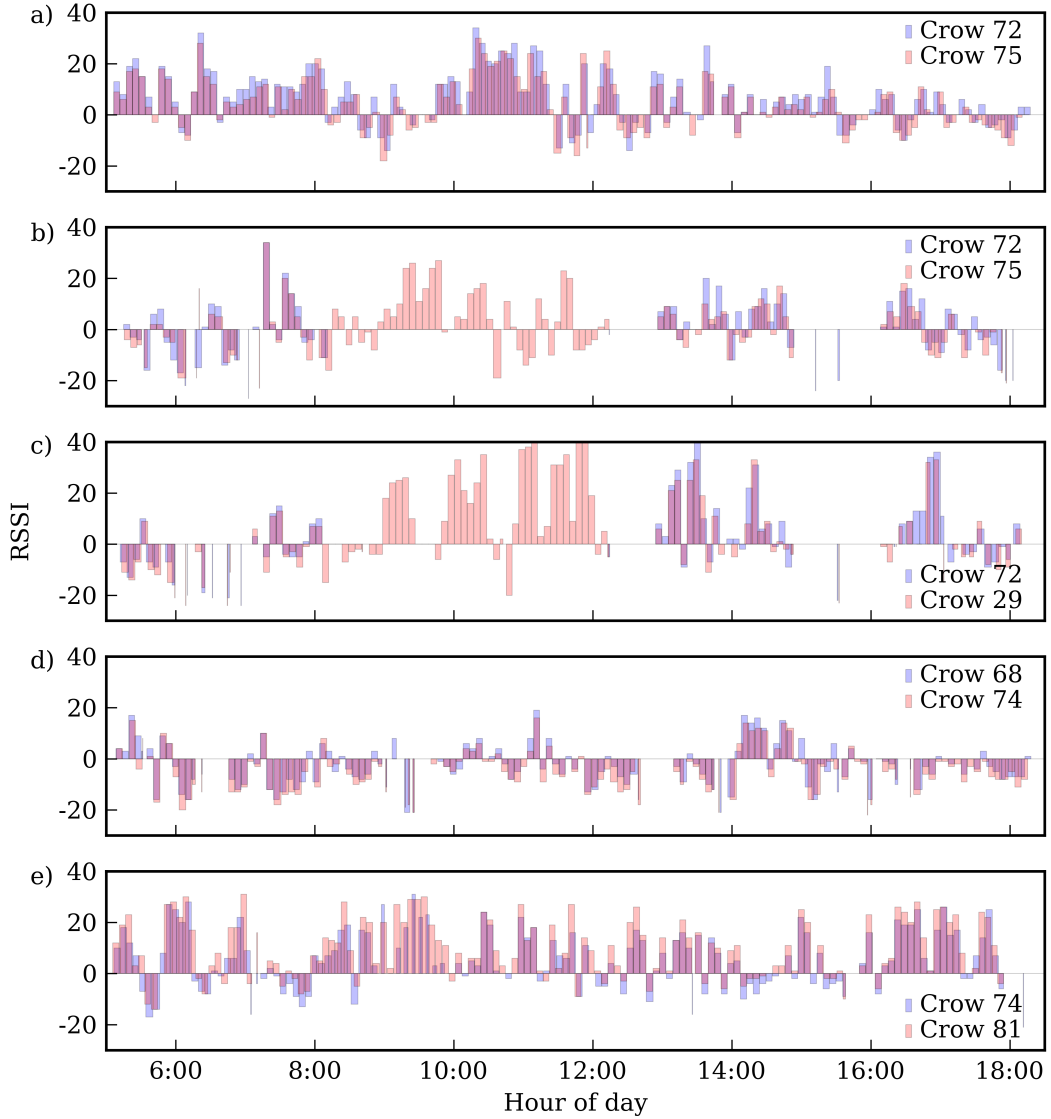


Figure 7.7: *Examples of reciprocal encounters. Each plot shows the $RSSI_{mean}$ values of all encounters between a pair of crows during a single day. a) Encounters logged between crow 72 (blue) and crow 75 (red) on day 19. In general the signal strength recorded by 72 was greater than that recorded by 75. b) and c) show two sets of reciprocal encounters on day 5 both involving crow 72 (blue). These show that tag 72 failed to receive any signals during the later half of the morning. d) and e) show two further examples on days 18 and 19 respectively. Again these show that most of the time one of the tags consistently records a higher signal strength than the other. It is also possible to see the disparity in start and end times of reciprocal encounters particularly between 9:00 and 10:00 in e).*

be *amalgamated* to produce a single timeline of encounters between each pair of crows. Since there were no calibration experiments performed to gauge the relative sensitivities of tags there is no way of reliably calculating what the ‘correct’ signal strength should be for encounters. The lack of tag calibration also makes it impossible to know which tags are more accurately recording start and end times of encounters and apart from this nothing is known about the tag height above the ground, relative orientation of the two tags or the habitat where the encounter took place, all of which affect tag performance (Rutz et al. 2012). I have therefore used the simplest way of reconciling reciprocal encounters which does not require any independent knowledge about the tags.

The first step in amalgamating reciprocal encounters is to apply a filter criterion (FC) to discard unwanted encounters. We are interested in investigating the potential for social learning of tool making skills so the analysis needs to be restricted to encounters where this may be possible. Crows need to at least be able to observe each other in order for social learning to take place and so only close range encounters are retained. The FC used to achieve this is $\text{RSSI}_{\text{mean}} \geq 15$ which corresponds to a proximity of ~ 5 m (Burns et al. in prep.).

The steps taken to amalgamate reciprocal encounters are shown in Figure 7.8 which shows real data between tags 74 and 81 on day 14 between 5:15–7:15 hrs. In this example I have amalgamated the $\text{RSSI}_{\text{mean}}$ values of signals transmitted by tag 74 and received by tag 81 (shown in blue) with signals transmitted by tag 81 and received by tag 74 (shown in red) (Figure 7.8a). After discarding all encounters which do not meet the FC this leaves 8 encounters, 6 received by tag 81 and 2 by tag 74 (Fig. 7.8b).

The first two encounters shortly after 5:30 are an example of two encounters separated by a brief gap (Fig. 7.8b). As mentioned in the previous section this is a result of the programmed limit of log files to close after a maximum of 300 s. In order to be able to analyse the total length of time in which crows remain within range I have concatenated consecutive encounters which are separated by a gap less than 23 s.

Figure 7.8c shows the result of amalgamating the reciprocal encounters. To do this I have defined two crows to be engaged in an encounter at any time when either tag is receiving a signal from the other tag. This has resulted in 4 encounters

between crows 74 and 81 for which the $\text{RSSI}_{\text{mean}}$ value is greater than or equal to 15. Figure 7.8c is an example of what I shall call a *timeline* plot. In such plots the timeline of a crow is represented by a black horizontal line and green shading between two timelines indicates a period in which the two crows are engaged in an encounter.

The process of amalgamation concatenates consecutive encounters if the intervening gap is less than 23s. The amalgamated encounters can therefore be longer than the 300s limit programmed into the tags. Figure 7.9 shows the effect of amalgamating encounters on the distribution of durations. Whilst the majority of logged encounters are between 5–6 min long, amalgamation at $\text{FC } \text{RSSI}_{\text{mean}} \geq 15$ shows that crows spend up to ~ 11 min in close proximity of each other.

7.3.2 Static and temporal network visualisation

To get an overall view of the crows’ association patterns it is useful to visualise the data in a range of different ways. A good starting point for visualisation is to construct some network diagrams of the data. A static network can be obtained from temporal network data by aggregating over a specified time interval (Holme and Saramäki 2012). This can be done in a variety of ways but since the aim here is to gain an overview of crows’ association preferences I have weighted edges by the total duration of all encounters between each pair of crows within the time interval. The choice of time interval depends on the level of detail being investigated. A series of hourly time intervals over the course of one day could be informative as to the crows’ habits during the course of one day. A coarser time interval of one day allows the total associations during each day to be compared with each other. The time interval chosen is arbitrary but one day is a reasonable starting point for investigation.

Figure 7.10 shows four network diagrams where the encounters have been aggregated over each of the four experimental periods. Encounters here have been filtered to include only those of close range ($\text{RSSI}_{\text{mean}} \geq 15$) and nodes have been coloured according to crow capture site. The layout of the nodes has been calculated using the Kamada-Kawai algorithm (Kamada and Kawai 1989) implemented in the Python igraph package (Csardi and Nepusz 2006) which represents each network edge as a spring with length dependent on the edge weight. The

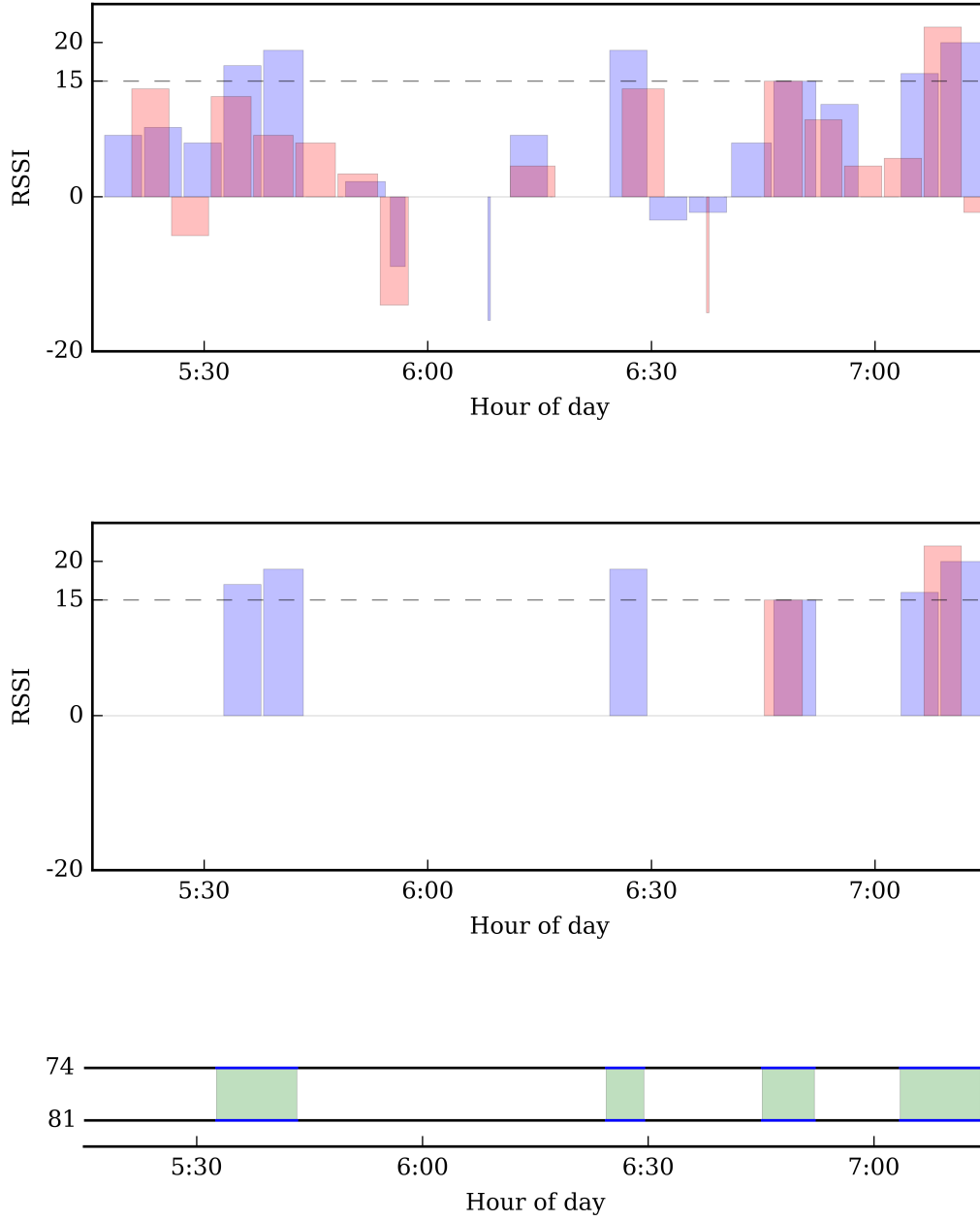


Figure 7.8: Steps taken to amalgamate pairs of reciprocal encounters. a) shows $RSSI_{mean}$ values for all encounters between crows 81 and 74 on day 14 between 5:15–7:15 as recorded by tag 81 (blue) and tag 74 (red). Amalgamation is performed at a given filter criterion (FC). Here the requirement is that $RSSI_{mean} \geq 15$. The filter level is indicated in a) and b) by the dashed line. The first step is to discard all encounters which do not fulfil the FC. The result of this is shown in b). Using the remaining data, two crows are defined to be engaged in an encounter at any time when either tag is receiving a signal from the other tag. c) shows a timeline plot indicating with green shading the times at which there is an encounter between crows 74 and 81. Consecutive encounters separated by a gap less than 23 s have been concatenated.

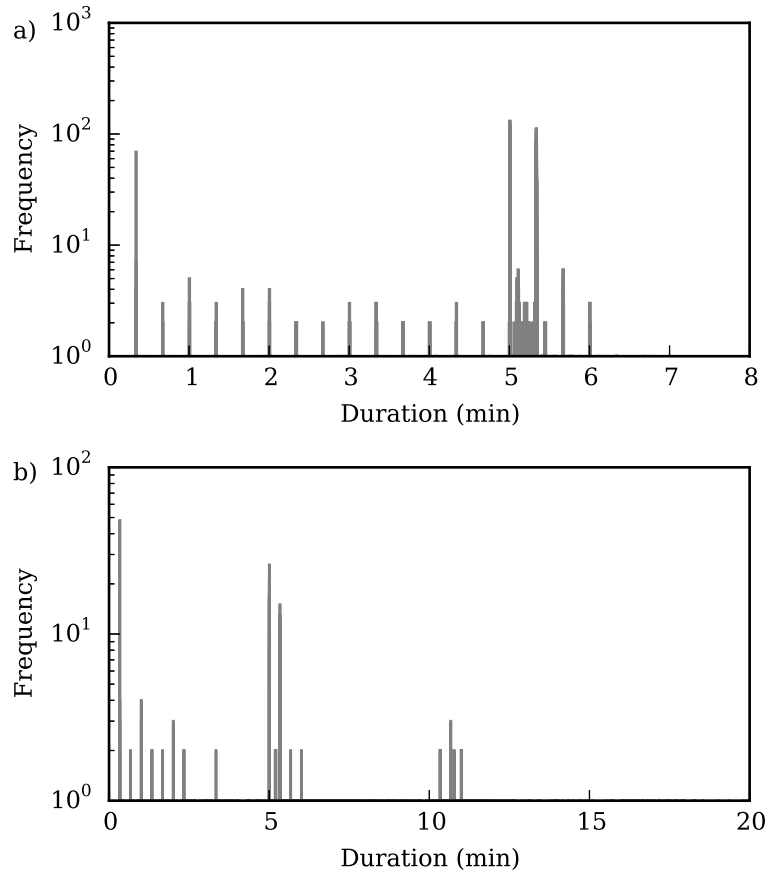


Figure 7.9: *The effect of amalgamation on encounter durations. a) Distribution of encounter durations for all encounters which satisfy the $FC\ RSSI_{mean} \geq 15$. b) Distribution of durations after amalgamating all encounters at the same FC.*

locations of the nodes are then adjusted to minimise the energy in the system so that nodes which are strongly linked end up closer together than weakly linked nodes. The algorithm was run using data aggregated over all 19 study days and the resultant layout was then used for all four networks. The layout and node colours make it visually apparent that the captured crows fall into two communities which correspond to the capture sites of Pig and Magic. Crow 85, which was captured at Tabou, has strong associations only with crows captured at Pig and so for the remainder of this chapter it will be assigned to the Pig community. The division of the crows into the communities of Pig and Magic is mainly for analysis purposes as it may not represent any true segregation in the wild. It is possible that by sampling the wild population mainly at Pig and Magic other crows which inhabit the area in between were missed so that the wild population is not actually segregated. However for this study it remains important to notice

the apparent communities in the data and treat them separately as there are clearly far more intra than inter community encounters recorded.

The complete temporal data can be displayed on timeline plots as introduced in the previous section. These plots are based on timelines of interval graphs shown in Holme and Saramäki (2012). The layout of timeline plots can be manipulated in order to make any structure in the data more apparent. To illustrate this Figure 7.11 shows two timeline plots of the same data with different orderings of crows along the y-axis. Figure 7.11a orders the crows according to ascending tag ID. This is not visually appealing as many shaded green blocks representing encounters overlap with each other. One way to improve on this is to reorder the crows by placing crows which associate frequently with each other closer together and crows which associate with each other fewer times further apart. The optimum layout for this premise can be found by minimising the total area of green shading on each plot. Figure 7.11b shows the same data with the crows ordered in order to minimise the total area of green shading over all B days. It is easy to see that this layout makes the structure of the data much more apparent. This layout shows clearly that there were no inter-community close range encounters on day 7. The layout also reveals that there are several pairs or triplets of crows in Pig (e.g. adults 81 and 68 and immature 74) which engage in close range encounters with each other throughout the course of the day suggesting that these crows have strong bonds with each other. This structure is also repeated on other study days (see Appendix A for a timeline plot of each study day).

7.4 Emulation of information spreading

The spreading of information through the network was emulated using a simple SI model (details of the algorithm used are given in App. B.1). Emulations, which were initially run over one day's data, were initiated by supposing one crow to have a hypothetical piece of information at the start of the day. This crow will be called the *starting* crow. Information can then be transmitted from informed crow to uninformed crow during encounters facilitating the spread of information through the network. The speed and extent of the information spread is highly dependent on the choice of starting crow as different crows have widely varying frequencies and patterns of encounters. To take account of this the starting crow

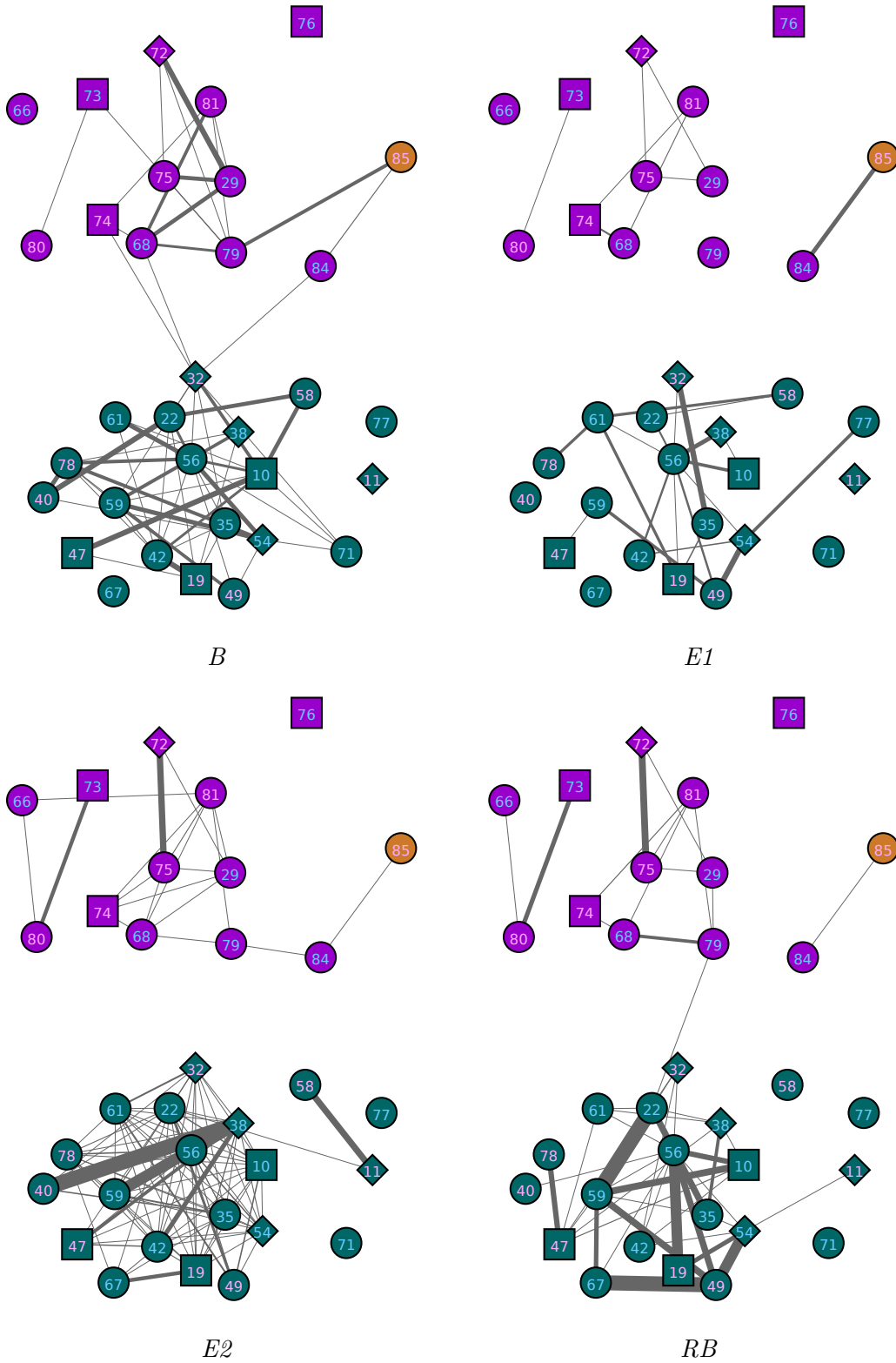


Figure 7.10: Time aggregated networks over a) B, b) E1, c) E2 and d) RB. Nodes are coloured according to capture site (Magic:green, Pig:purple, Tabou:orange) and are shaped according to age (adult:circle, immature:square, juvenile:diamond). Nodes are labelled by tag ID in pink for females and blue for males. Edge widths are scaled to represent the total duration of all encounters between two crows during the aggregation period.

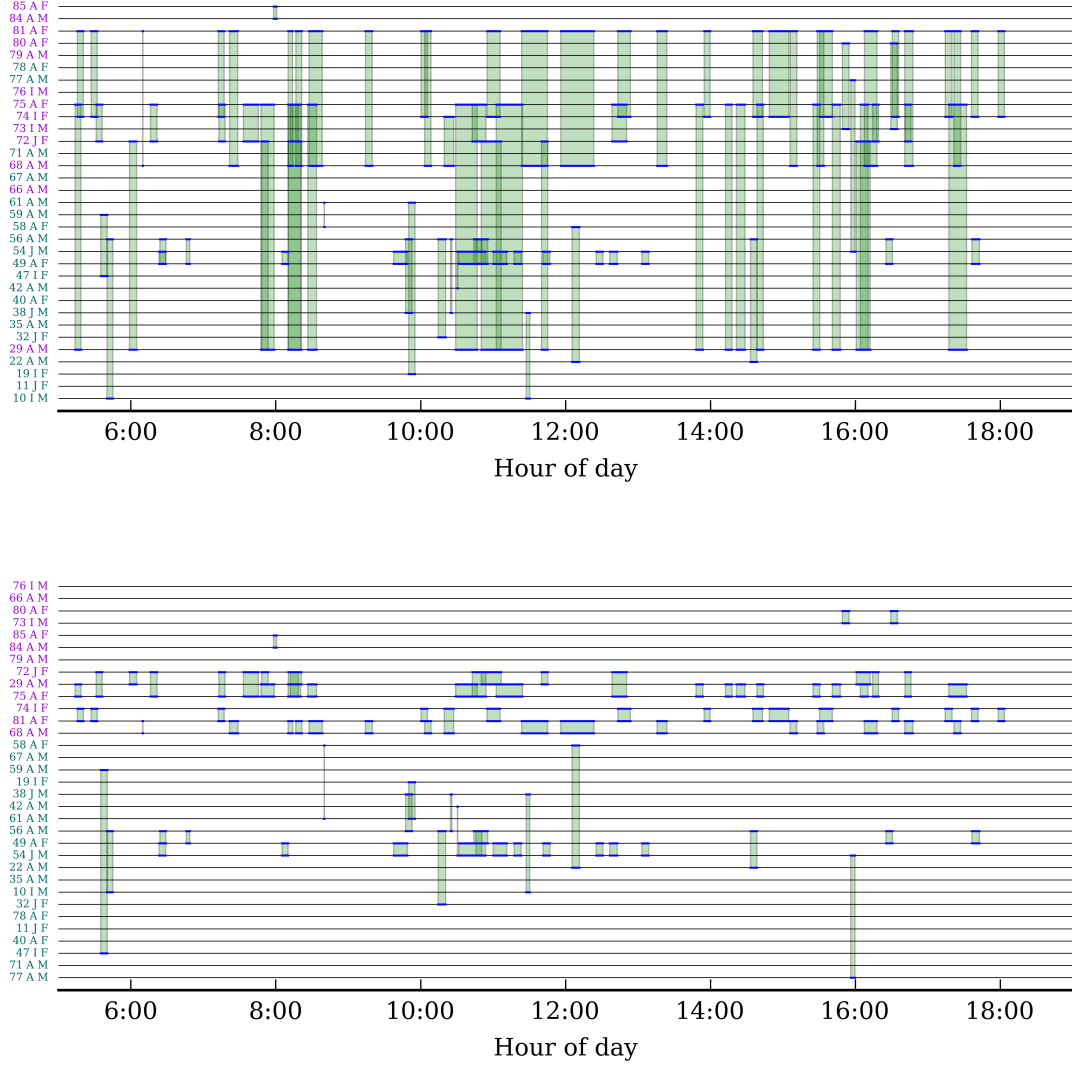


Figure 7.11: Timeline plots showing all encounters having $RSSI_{mean} \geq 15$ on day 7. The timeline of each crow is represented by a horizontal line and green shading between two timelines indicates the period in which two crows are engaged in an encounter. Each timeline is labelled with tag ID, age and sex and the labels are coloured according to community (Magic:green, Pig:purple). a) Crows are ordered according to tag ID. b) The ordering of crows has been calculated in order to minimise the total area of green shading over all B days.

was permuted and emulations were run using all possible starting crows. This allowed all information pathways which exist in the network to be analysed.

7.4.1 Waiting times and probability of transmission

To make the emulations more realistic information is not transferred instantaneously at the start of encounters. Instead a waiting time is introduced. Since information transfer in this study is intended to represent the learning of an aspect of tool manufacture or use by one crow watching another it is reasonable that this should take some period of time. It is also reasonable to introduce random variation to the length of the waiting time as in reality there will be variation in the length of time it takes to transfer information from crow to crow. Since waiting times are a random process, each emulation is performed multiple times in order to capture the variations in information pathways that this produces.

In order to achieve these specifications information transfer has been modelled as a Poisson process. This means there is a constant probability of information transfer in each second (Γ) and therefore the probability of information transfer in any particular second is not dependent on anything which has happened before then. The rest of this section covers the main features of Poisson processes and derives the probability that information will be transferred during the i th encounter (p_i).

The waiting times between events in a Poisson process follow an exponential distribution

$$f(t, \lambda) = \lambda e^{-\lambda t} \quad (7.1)$$

where t is the time between events and λ is a constant characterising the Poisson process. The probability of information transfer during each second is

$$\Gamma = \frac{1}{\lambda}. \quad (7.2)$$

This exponential distribution has the property that the mean number of seconds taken for information to be transferred is λ and its variance is λ^2 .

During one day there are m encounters between crow A and crow B each of length

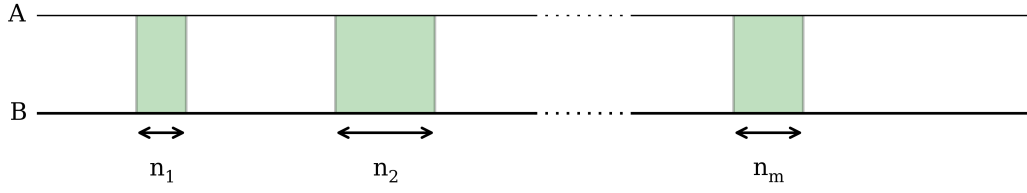


Figure 7.12: Timeline plot of m encounters between crows A and B. Each encounter has a duration of n_i seconds.

n_i seconds (Fig. 7.12). The probability of information transfer during 1 encounter can be calculated by summing the probabilities of information transfer during each second of the encounter. The probability of information transfer during the i th encounter is the sum of the probability of information transfer during each second of the encounter. Defining Γ to be the probability of information transfer during 1 second, this gives the probability of information transfer during the i th encounter (p_i) as

$$\begin{aligned}
 p_i &= \Gamma + (1 - \Gamma)\Gamma + \cdots + (1 - \Gamma)^{n_i-1}\Gamma \\
 &= \Gamma [1 + (1 - \Gamma) + (1 - \Gamma)^2 + \cdots + (1 - \Gamma)^{n_i-1}] \\
 &= 1 - (1 - \Gamma)^{n_i} \\
 &= 1 - \left(1 - \frac{1}{\lambda}\right)^{n_i}.
 \end{aligned} \tag{7.3}$$

The dependence of p_i on λ and n_i is shown in Figure 7.13. For the modal encounter duration of 5 min the probabilities of information being transferred are $p=0.99$, 0.63 and 0.39 for $\lambda=1$ min, 5 min and 10 min respectively.

7.4.2 Choosing an appropriate λ

A sensible value should be picked for λ although the choice is ultimately arbitrary. The value of λ can be chosen by considering the key timescales in this study. Firstly the durations of encounters, which after amalgamation can be up to ~ 11 min long although the majority are around 5 min (Fig. 7.9). Secondly, it is reasonable to think that information transfer may need a timescale of at least the order of a few minutes as performing foraging behaviour will take at least this long. Thirdly, in order to make the best use of the collected data it is appealing to choose a λ which allows the outdomain at the end of 1 day to

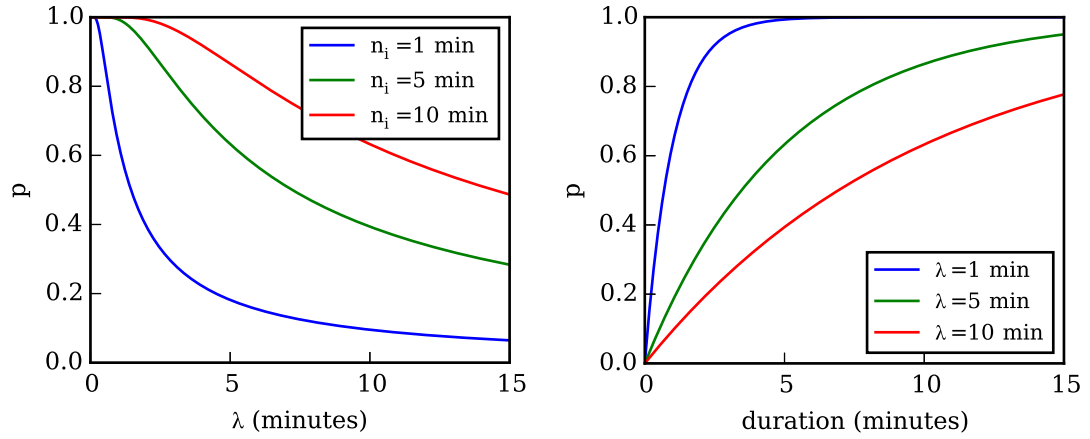


Figure 7.13: Probability of information transfer during one encounter as a function of a) λ and b) duration.

reach the majority of the connected network. The probabilities of information transfer via different pathways through the network will then be differentiated by the random variation in λ .

Choosing $\lambda = 5$ min is long enough for foraging behaviour to be observed and short enough to analyse information flow over 1 day. This is the value which has been used in the rest of this chapter. Sensitivity analysis was performed using λ s in the range of 20 sec – 12 hrs. Outdomain sizes were found to vary slowly with λ such that varying λ by ± 3 min caused outdomain sizes averaged over all crows to vary by less than one crow.

7.4.3 Emulation examples

Two examples of emulations are shown in Figure 7.14. The information pathways produced by the emulation have been superimposed on timeline plots using red arrows to indicate information transfer events and colouring a crow's timeline yellow when it has been informed. These visualisations show clearly the times at which emulated information transfer happens and which crows inform which others. The plots also show the *outdomain* which is defined as the set of crows which has been informed by the end of the day. The concept of the outdomain is used throughout this chapter as it is a simple way of defining the extent of information spread.

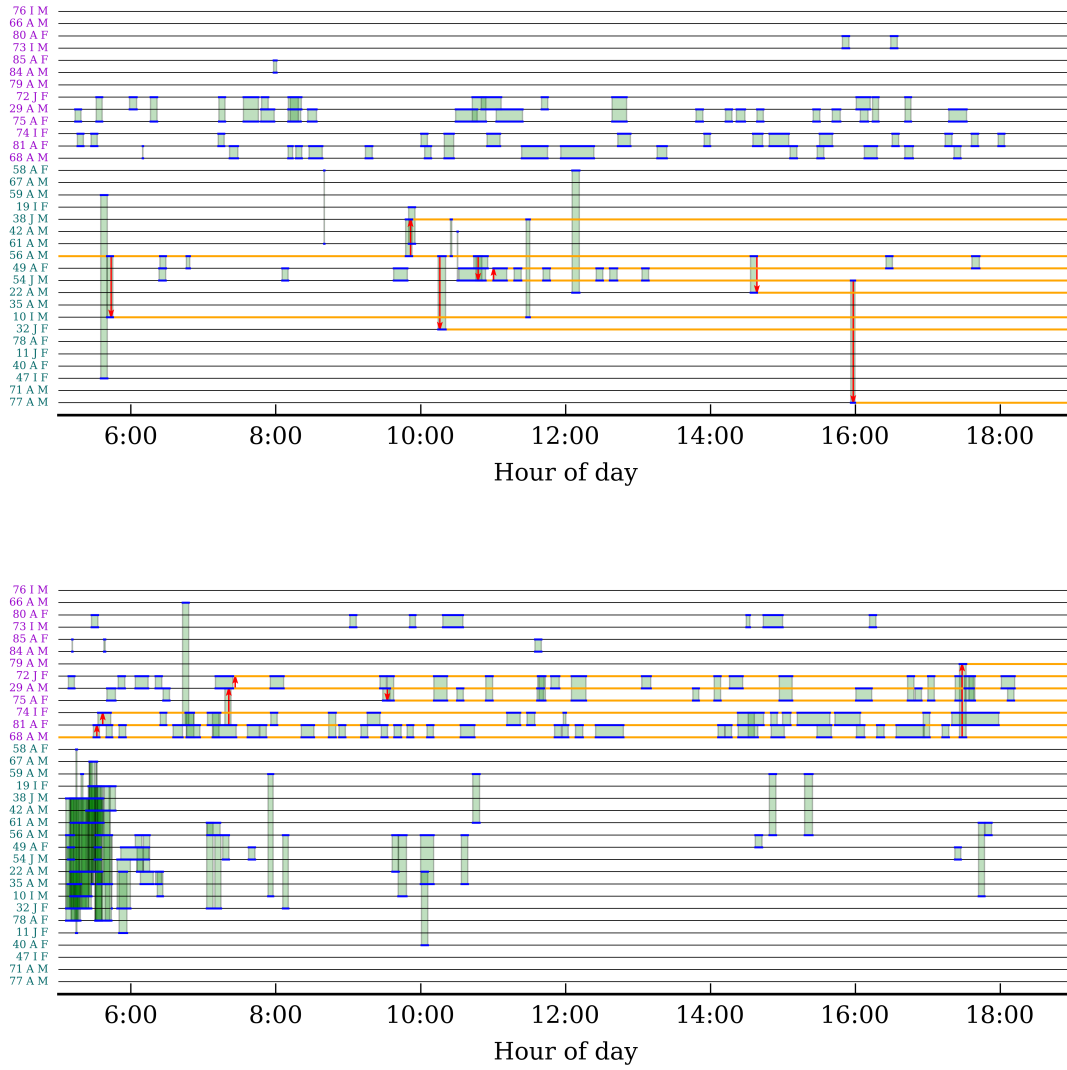


Figure 7.14: Two examples of daily timelines with emulations superimposed. Instances of information transfer from one crow to another are shown with red arrows from the informant to the recipient and crow timelines are coloured yellow after the time at which the crow becomes informed. a) Emulation starting with crow 56 on day 8. b) Emulation starting with crow 68 on day 14.

7.4.4 Emulations on an equivalent static network

As mentioned in Section 2.3, a far more accurate picture of dynamics on the network can be produced when timestamped edge data are available. To demonstrate this I have compared emulations on the temporal network with emulations run on an equivalent static network. The key difference is that in the temporal network encounters are ordered in time and this ordering constrains the order in which crows become informed and also limits the speed of information flow. In other words, by using a static network I am removing causality and seeing how much of a difference that makes to the potential information flow. The procedure for running emulations on a static network is slightly different to the temporal case and is described in Appendix B.2.

The condition defining the equivalence between the static and temporal cases is that the total probability of information being transferred over the whole day (P_{AB}) between a given pair of crows should be equal in both networks. This is achieved by calculating P_{AB} for the temporal network and calculating an effective λ' for each edge in the static network such that the probability of information being transferred in each second is a constant and the total probability of information transfer over the N seconds in the day is equal to P_{AB} .

If there are m encounters between crows A and B in the course of the day then P_{AB} can be written down as

$$\begin{aligned} P_{AB} &= p_1 + q_1 p_2 + q_1 q_2 p_3 + \cdots + q_1 \cdots q_{m-1} p_m \\ &= (1 - q_1) + q_1 (1 - q_2) + q_1 q_2 (1 - q_3) + \cdots + q_1 \cdots q_{m-1} (1 - q_m) \\ &= 1 - q_1 q_2 \cdots q_m \end{aligned} \tag{7.4}$$

where q_i is the probability of information *not* being transferred during the i th encounter. From Equation 7.3,

$$\begin{aligned} q_i &= 1 - p_i \\ &= \left(1 - \frac{1}{\lambda}\right)^{n_i}. \end{aligned}$$

Substituting this into Equation 7.4 gives

$$\begin{aligned} P_{AB} &= 1 - \left(1 - \frac{1}{\lambda}\right)^{n_1} \left(1 - \frac{1}{\lambda}\right)^{n_2} \dots \left(1 - \frac{1}{\lambda}\right)^{n_m} \\ &= 1 - \left(1 - \frac{1}{\lambda}\right)^{n_1+n_2+\dots+n_m}. \end{aligned}$$

The total probability of information transfer in the static network P'_{AB} is

$$P'_{AB} = 1 - \left(1 - \frac{1}{\lambda'}\right)^N$$

where there are N seconds in the day. Equating P_{AB} with P'_{AB} and solving for λ' gives

$$\lambda' = \left(1 - \left(1 - \frac{1}{\lambda}\right)^{\frac{n_1+n_2+\dots+n_m}{N}}\right)^{-1}.$$

The value of λ' will be different for each edge in the static network as the total duration of encounters between each pair of crows varies.

Using the calculated λ' for each edge, emulations can be run on the equivalent static network in a way analogous to those run on the temporal network. Information is passed from informed to non-informed crows along network edges with waiting times calculated using λ' . An emulation is allowed to run for the duration of one day and the outcome is examined at the end of the day. For the static network information transfer events can happen at any time throughout the day whereas for the temporal network they are confined to occurring during the times of encounters.

Figure 7.15 compares an emulation run on the temporal network (Fig. 7.15a) with the same emulation run on the equivalent static network (Fig. 7.15b). To make the comparison easier both emulations have been superimposed upon the timelines of encounters during the day. In this example the outdomain size for the temporal network is 4 whereas in the static network twice as many crows are informed by the end of the day and the outdomain size is 8. This example shows how the time ordering of events in the temporal network has caused the outdomain to be smaller. Figure 7.15b shows crow 38 receiving information in the static network emulation via the path $56 \rightarrow 61 \rightarrow 38$. In the temporal network emulation crow 61 becomes informed near 11:00 hrs and the only encounters

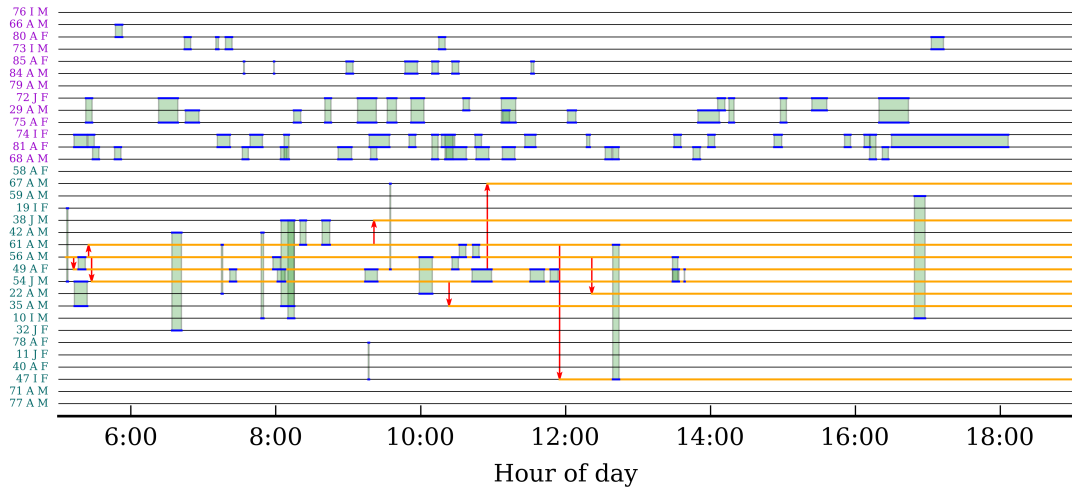
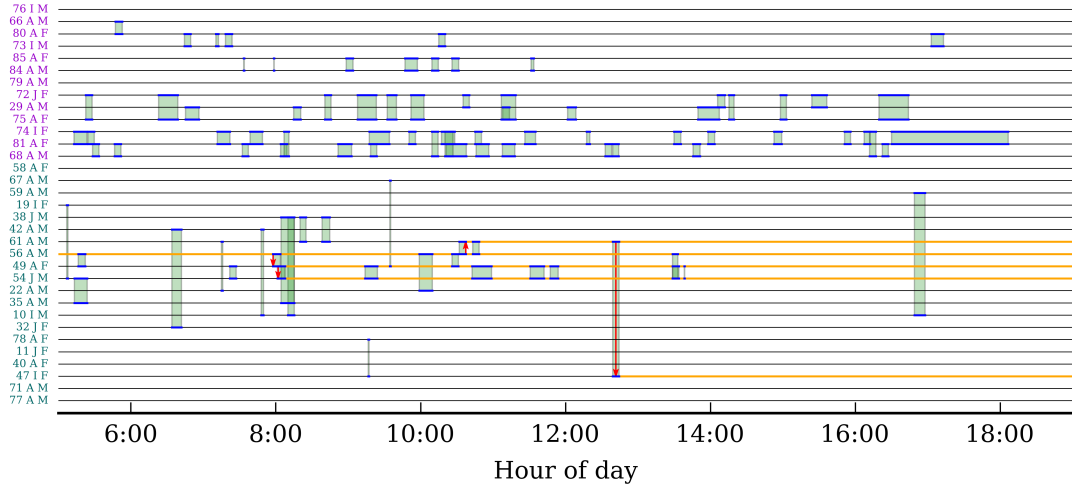


Figure 7.15: Comparison of an emulation run on day 15 starting with crow 56 on a) the temporal and b) the static network. Both emulations have been superimposed upon the timelines of encounters for day 15.

between 61 and 38 are between 8:00–9:00 hrs. The time ordering of these events therefore makes the path $56 \rightarrow 61 \rightarrow 38$ impossible in the temporal network.

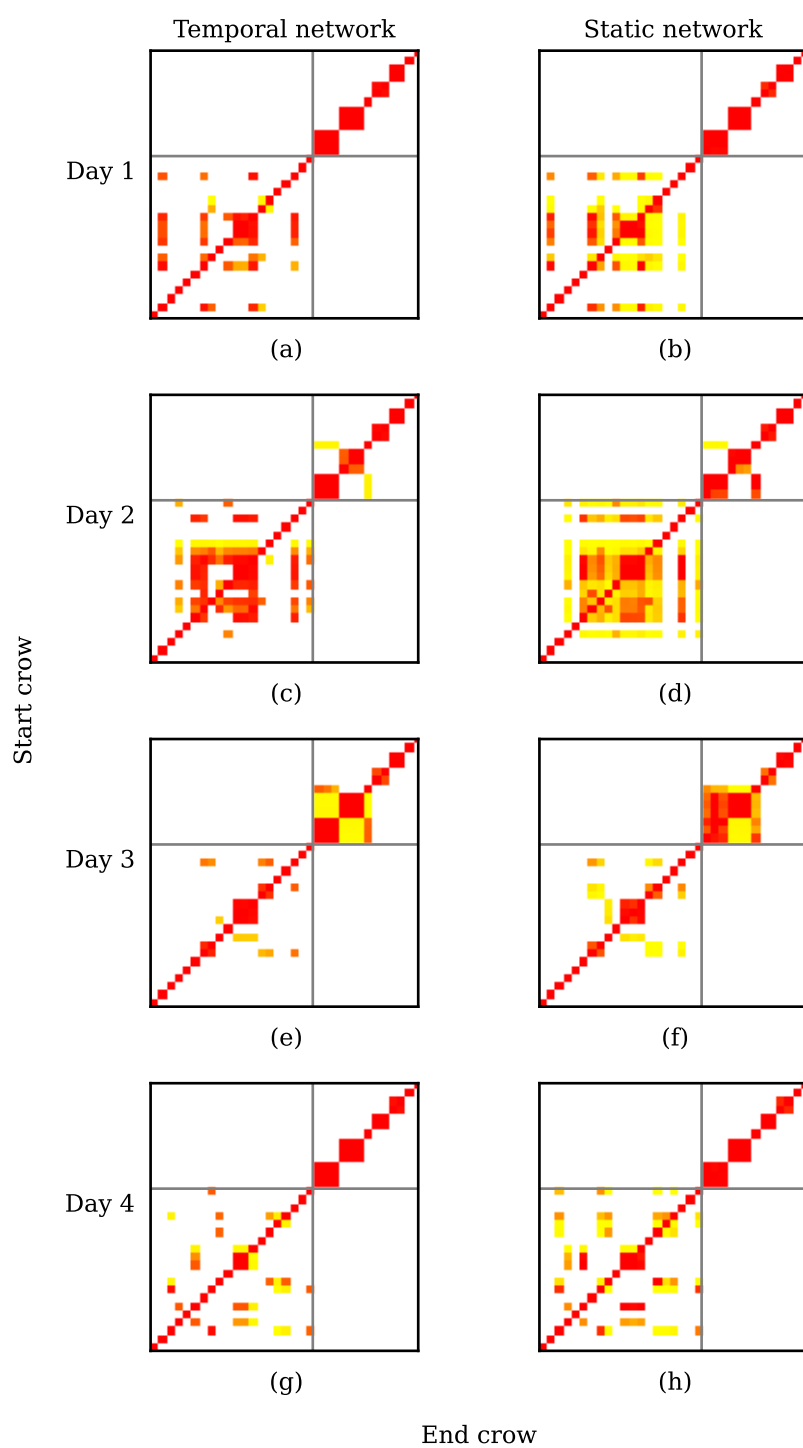
7.5 Results

7.5.1 Potential for information spreading during Baseline

Emulations can be visualised using matrix plots (Fig. 7.16). Each matrix in Figure 7.16a–n displays the results from 1000 emulations starting with each crow on a particular day. Each cell (i, j) is coloured according to how often crow i is in the outdomain of crow j . The colour scale runs from white, meaning crow i is never in the outdomain of crow j , to red, meaning crow i was in the outdomain of crow j in 100% of emulations starting with crow j . Crows are arranged along the axes in the same order as in the timeline plots (Fig. 7.14) and grey cross lines have been placed so that Magic \rightarrow Magic emulations are in the bottom left quadrant, Pig \rightarrow Pig in the top right, Magic \rightarrow Pig in the bottom right and Pig \rightarrow Magic in the top left.

Matrix plots demonstrate the potential for information to spread through the network. The row sums indicate the average outdomain for each crow. The sums of the columns represent the complementary statistic indomain, the number of starting crows from which a particular ending crow could have received information during the day. Figure 7.16 (left hand column) shows how the patterns of encounters on each day affect information flow through the network. There is a clear difference in the information flow potential between the two communities Magic and Pig. The spread of information in Pig is mainly confined to small subgroups of 2 or 3 crows (Fig. 7.16a, c, g & m). These subgroups could potentially be family groups and this will be considered in Section 7.5.3. In Magic the pattern of information spread varies much more from day to day.

The corresponding emulations run on the static network (Fig. 7.16 right hand column) show that in general information is spread to a greater number of crows by the end of the day than on the temporal network. This is most pronounced for emulations run in Magic on days 2 and 6. These differences demonstrate



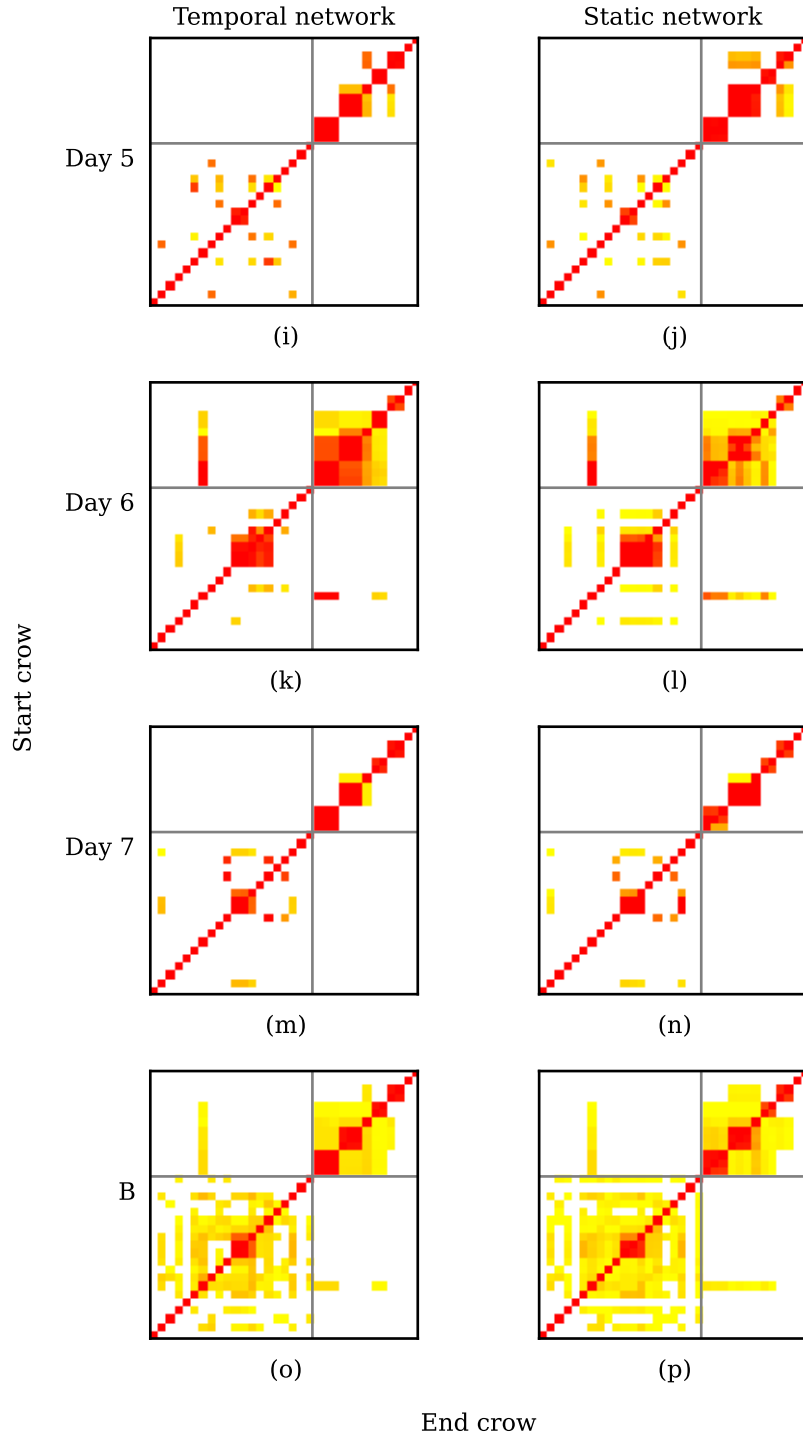


Figure 7.16: Matrix visualisations of emulations run on the temporal network (left hand column) and static network (right hand column) during B days. Each cell (i, j) is shaded from white to red according to the percentage of emulations in which crow i is in the outdomain of crow j , 0–100% respectively. Grey cross lines separate crows from communities Magic (bottom left) and Pig (top right).

that running emulations on static network data leads to less accurate analysis of potential information flow.

Figures 7.16o & p show the combined results of emulations over all B days. The number of shaded cells in these matrices is far greater than the number of shaded cells in any individual day showing that crows do not associate with the same set of other crows on every day.

7.5.2 Effects of experimental manipulation on network structure and information flow

Two manipulations were carried out over the course of the study (Sec. 7.2.3). In the first experiment E1, a section of candlenut tree was placed midway between capture sites Magic and Pig. After three days this was removed and E2 commenced by placing a section of candlenut tree at the centre of each of Magic and Pig. After four days these were removed and the system was observed for five further days which constituted the RB period. The timeline plots in Appendix A show all encounters having $RSSI_{\text{mean}} \geq 15$ during every day in the study. These do not show any qualitative change between the encounters in E1 and those in B. There is however a marked change during E2. On days 10–13 there is an obvious increase in activity between crows from Magic during the early morning. There appears to be no such change in crows from Pig.

The increase in activity in Magic is also visible in the time aggregated networks for each period shown in Figure 7.10. Here it can be seen that there were many more edges between crows from Magic during E2 than in the other experimental periods. Figure 7.17a–c shows how statistics from daily aggregated networks vary over the course of the study. In Magic the number of network edges per day is around 5 times higher during E2 than in B or E1. There is also an increase in the total duration of encounters in Magic on each day however there is no increase in the total duration per edge. Together these factors indicate that crows in Magic associate with a greater number of other crows during E2 but on average do not increase the amount of time spent with each crow. E2 does not produce this effect in Pig.

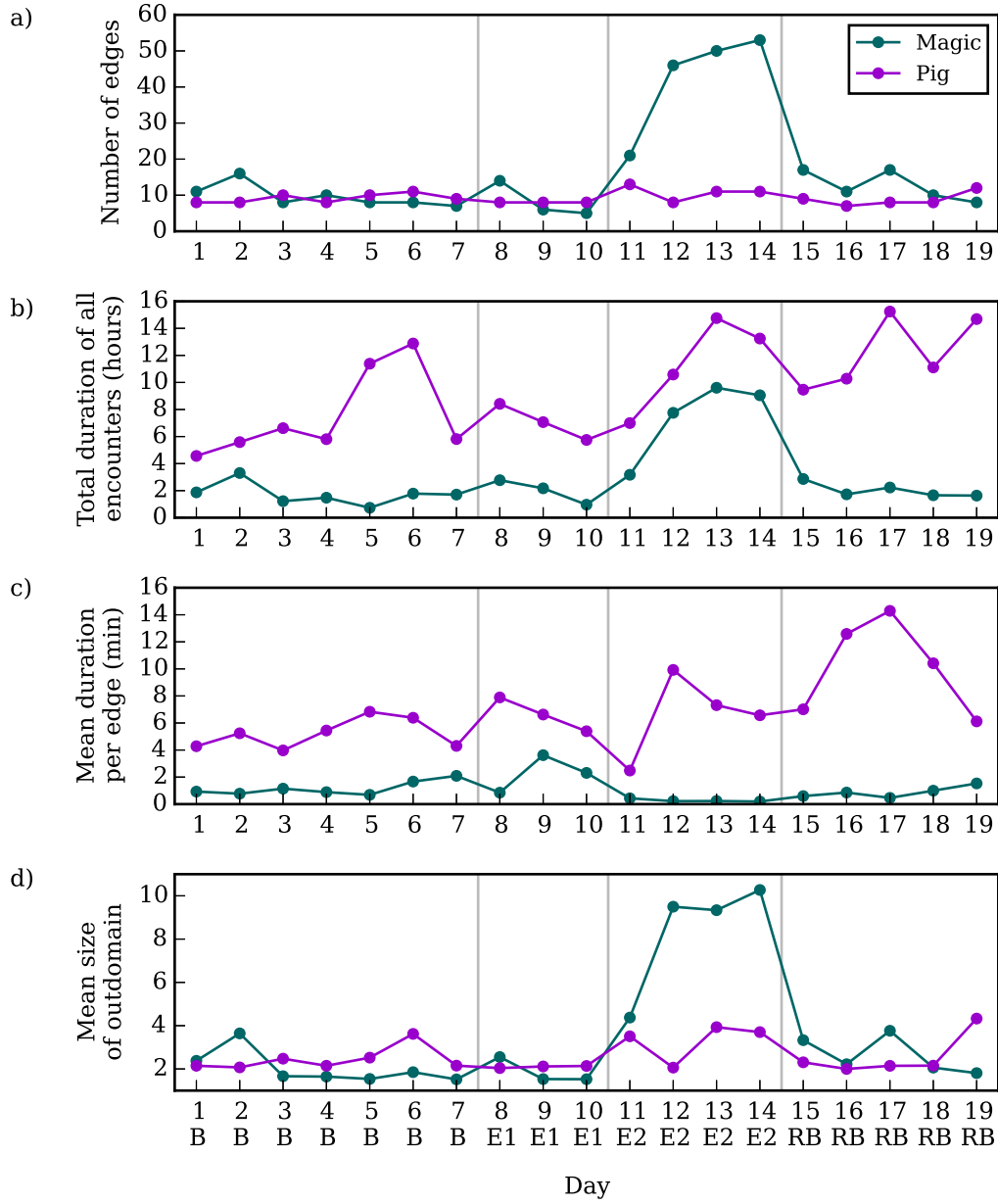


Figure 7.17: Variation in network measures over the course of the study. a) Number of network edges on each day. b) Total duration of all encounters. c) Mean duration of encounters along each network edge. d) Size of outdomain averaged over all starting crows.

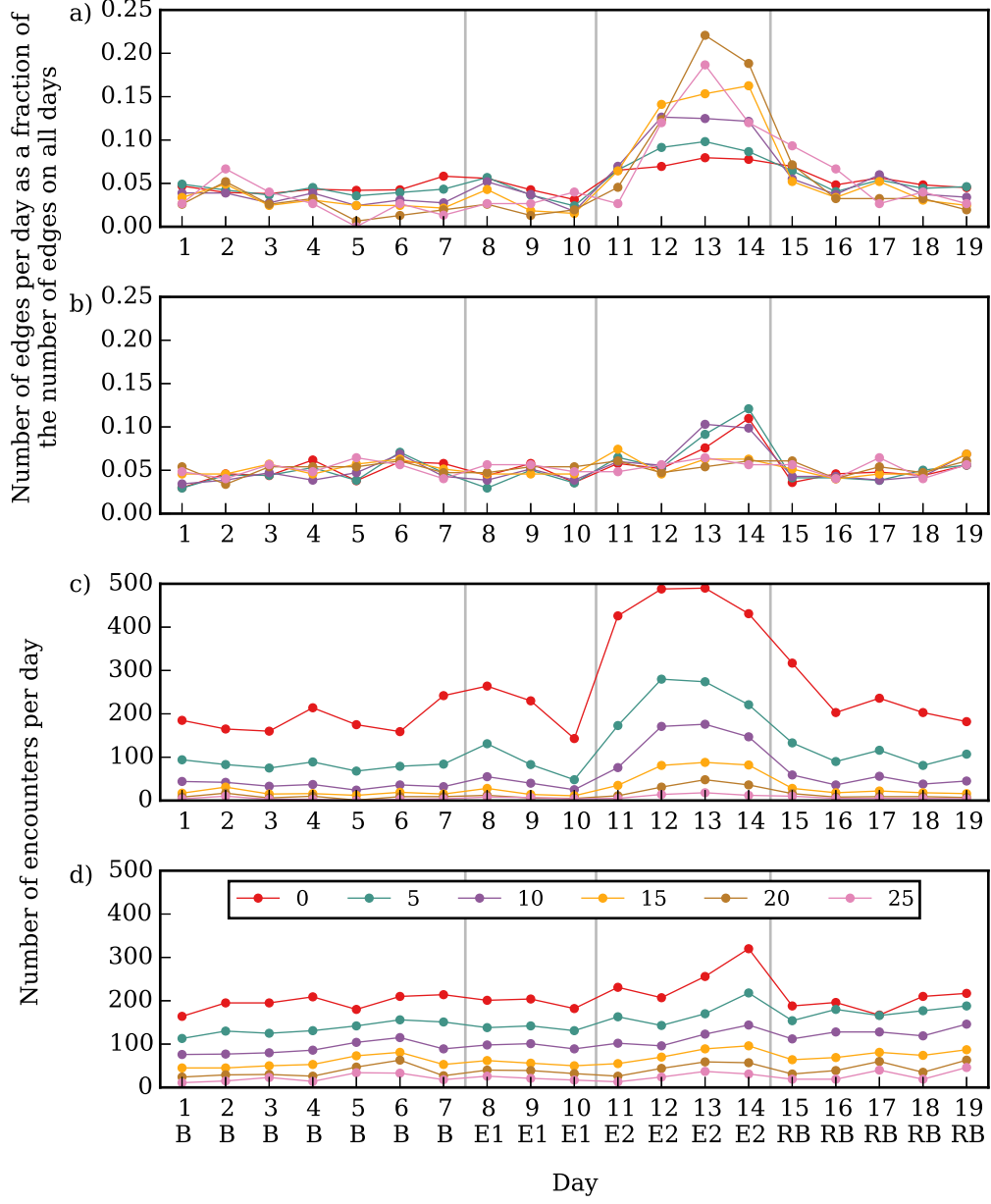


Figure 7.18: Variation in network statistics over the study for different filters ($RSSI_{mean} \geq 0, 5, 10, 15, 20$ & 25). Number of edges on each day as a fraction of the total over all study days in a) Magic and b) Pig. Number of encounters per day in c) Magic and d) Pig.

Figure 7.18 shows the range of $\text{RSSI}_{\text{mean}}$ s over which the effect of E2 is present. Figure 7.18a shows that in Magic the greatest relative increase in the number of edges between E2 and B is seen at the stronger signal strengths of $\text{RSSI}_{\text{mean}} \geq 20$ followed by 25 and 15. Figure 7.18c shows however that increasing the filter level greatly reduces the number of encounters in the network. The average number of encounters per day in Magic on B days is 185.7 at a filter level of 0 which drops to 17.9 at $\text{RSSI}_{\text{mean}} \geq 15$ and to 8.8 at $\text{RSSI}_{\text{mean}} \geq 20$. At $\text{RSSI}_{\text{mean}} \geq 20$ the encounters are spread over an average of 3.9 edges on each B day whereas at $\text{RSSI}_{\text{mean}} \geq 15$ there are an average of 9.7 edges per day. Therefore even though the effect of E2 is greater at higher filter levels, $\text{RSSI}_{\text{mean}} \geq 15$ has been used throughout in order to avoid over filtering the network.

Figure 7.18b & d show corresponding plots for encounters within Fig. Figure 7.18b shows that there is a small increase in the number of edges in E2 in only the lower filters of $\text{RSSI}_{\text{mean}} \geq 0, 5 \text{ \& } 10$. These filter levels correspond to distances of up to $\sim 8 \text{ m}$ and $\sim 15 \text{ m}$ which are likely to be less relevant for information flow via social learning (Burns et al. in prep.).

The increase in number of edges and encounters in Magic E2 results in an increase in potential for information flow. Figure 7.19 visualises the results of running emulations during each period. Since the shortest period E1 is 3 days long, each matrix shows the accumulation of emulations from 3 days of each period. The days chosen are the ones closest to the start of E2 (B: days 5–7, E1: days 8–10, E2: days 11–13, RB: days 15–17). Each cell (i, j) is shaded red if crow i is in the outdomain of crow j in 100% of emulations starting on all 3 days and white if crow i is never in the outdomain of j . Figure 7.19 shows that in Magic the potential for information flow is similar in B and E1 but shows a large increase in E2. In RB the extent of the spreading has decreased from E2 but is still elevated above B levels. The average size of the outdomain (equivalent to the row sums in matrix plots) on each day is shown in Figure 7.17d. This shows the huge increase in outdomain size with E2 days having an outdomain on average 4.1 times larger than B days.

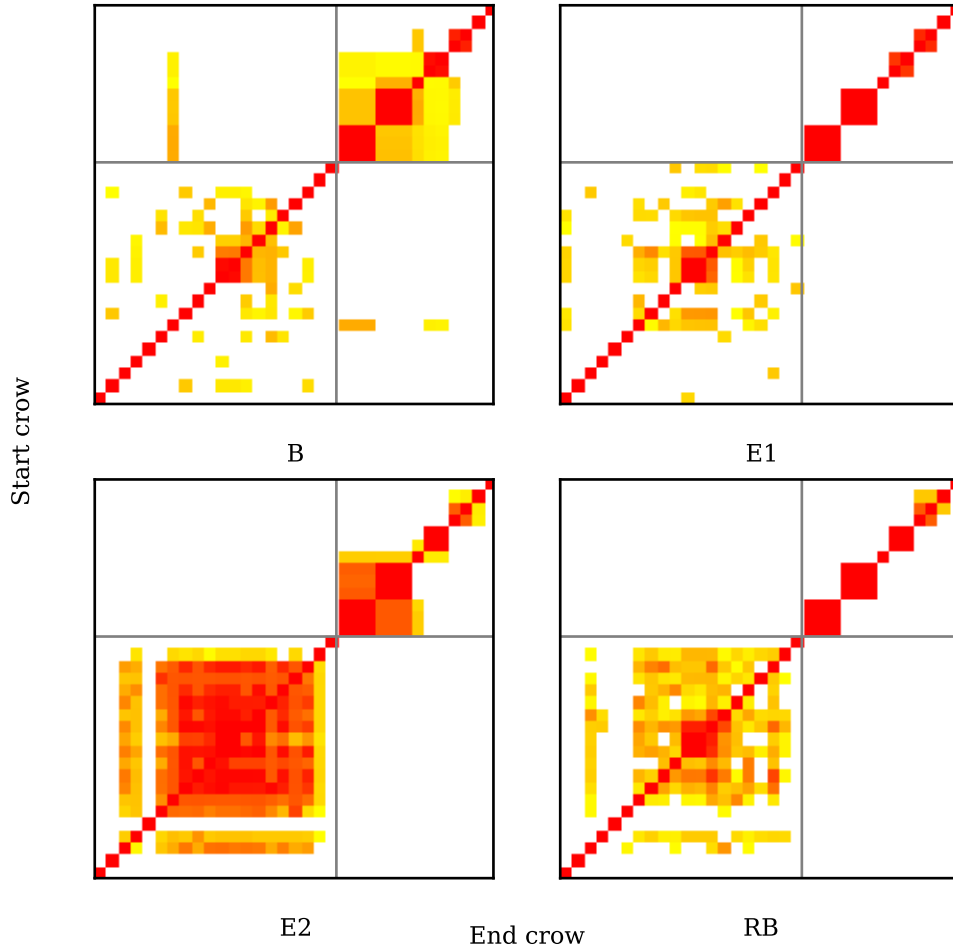


Figure 7.19: Matrix visualisations of emulations run on three days from each period (B: days 5–7, E1: days 8–10, E2: days 11–13, RB: days 15–17). Each cell (i, j) is shaded from white to red according to the percentage of emulations in which crow i is in the outdomain of crow j , 0–100% respectively. Grey cross lines separate crows from communities Magic (bottom left) and Pig (top right).

7.5.3 Potential for horizontal and oblique information flow

One aim of this study was to assess the potential for information to be passed between family groups. Information flow between families is called horizontal or oblique depending on whether information is passed within age classes or between them (e.g. adult to juvenile). In order to assess the information flow potential family groups had to be identified. Genotyping of crows provided information on whether pairs of crows were first order related and this revealed parent-offspring relationships. It is possible to identify a family group of 3 in this way as both parents will be first order related to the offspring. If however the offspring is not tagged, then it is harder to be sure of parent-parent relationships as they do not necessarily have any genetic relationship.

Figure 7.20a visualises the matrix of first order relations. Crows have been ordered using the same community based ordering as in previous figures so that relationships between crows in Magic are shown in the bottom left hand quadrant and those between crows in Pig in the upper right hand quadrant. Cells (i, j) are coloured purple if crow i is first order related to crow j . This visualisation shows that the communities Pig and Magic are not based on first order relatedness. The densities of first order related pairs (number of first order related pairs divided by total number of crow pairs) are 0.04 for Magic, 0.14 for Pig and 0.06 for inter-community pairs. 45% of the first order related pairs are inter-community.

One advantage of matrix plots is that the nodes can be rearranged to suit different purposes. In Figure 7.20b the nodes have been rearranged to place as many first order related crows next to each other as possible. This is a helpful arrangement for assessing whether information can flow between family groups. It is not possible to identify distinct families purely with relatedness data and so instead the most conservative informed guess has been used. The grey shaded areas indicate groups of crows in which every member is first order related to at least one other member. Whilst not every member of the group will be close family of each other member, it is likely that crows from different groups will not be close family.

Figure 7.20c displays the same emulation results shown in Figure 7.19 this time arranging the nodes according to relatedness. The grey shading of relatedness groups is also shown on these plots so that it is visually obvious which information

paths are between crows which may be in the same family and those which are between crows which are not in the same family. These plots demonstrate that there is potential in these networks for information to flow between families.

7.5.4 Information flow over longer timescales

All emulations presented so far have been run over a single day. Emulations were initiated by supposing one crow to have a hypothetical piece of information at the start of a day and the information flow through the network was tracked until the end of the day. All emulations have also used 5 min as the mean time for information to transfer from one crow to the next. This approach allowed temporal paths from each starting crow to each end crow to be differentiated in terms of their probability of transmitting information. It was often the case that information reached the maximum number of other crows possible within the day and so 1 day was sufficient for assessing the spread of the information.

One feature of the dataset which can either enable or hinder information spread over longer timescales is whether crows associate with the same crows on each day. Figure 7.21 shows that there is a wide range of behaviours amongst the crows. Each plot shows the amount of time that a subject crow spends with each other crow on each day of the study. The column corresponding to the subject crow is shaded grey. Other cells (i, j) are white if crow j had no encounters with the subject crow on day i , and are shaded yellow to red to indicate the total duration of encounters. The number of cells which are coloured yellow to red in one row indicates the subject crow's degree on that day.

Figures 7.21a & b show daily encounter durations for crows 49 and 54 respectively. These crows are first degree related, 49 being an adult female and 54 her juvenile female offspring. Although each of these crows associates with the other more frequently than with other crows, juvenile 54 associates with many more crows than adult 49. Furthermore 49 tends to associate with the same crows on different days (with 56 on 13 days, 59 on 4 days, 10 and 22 both on 2 days) whereas 54 associates with different crows on different days. In particular during the B, 54 encounters 6 crows other than 49 with 4 of those only being encountered on 1 day each.

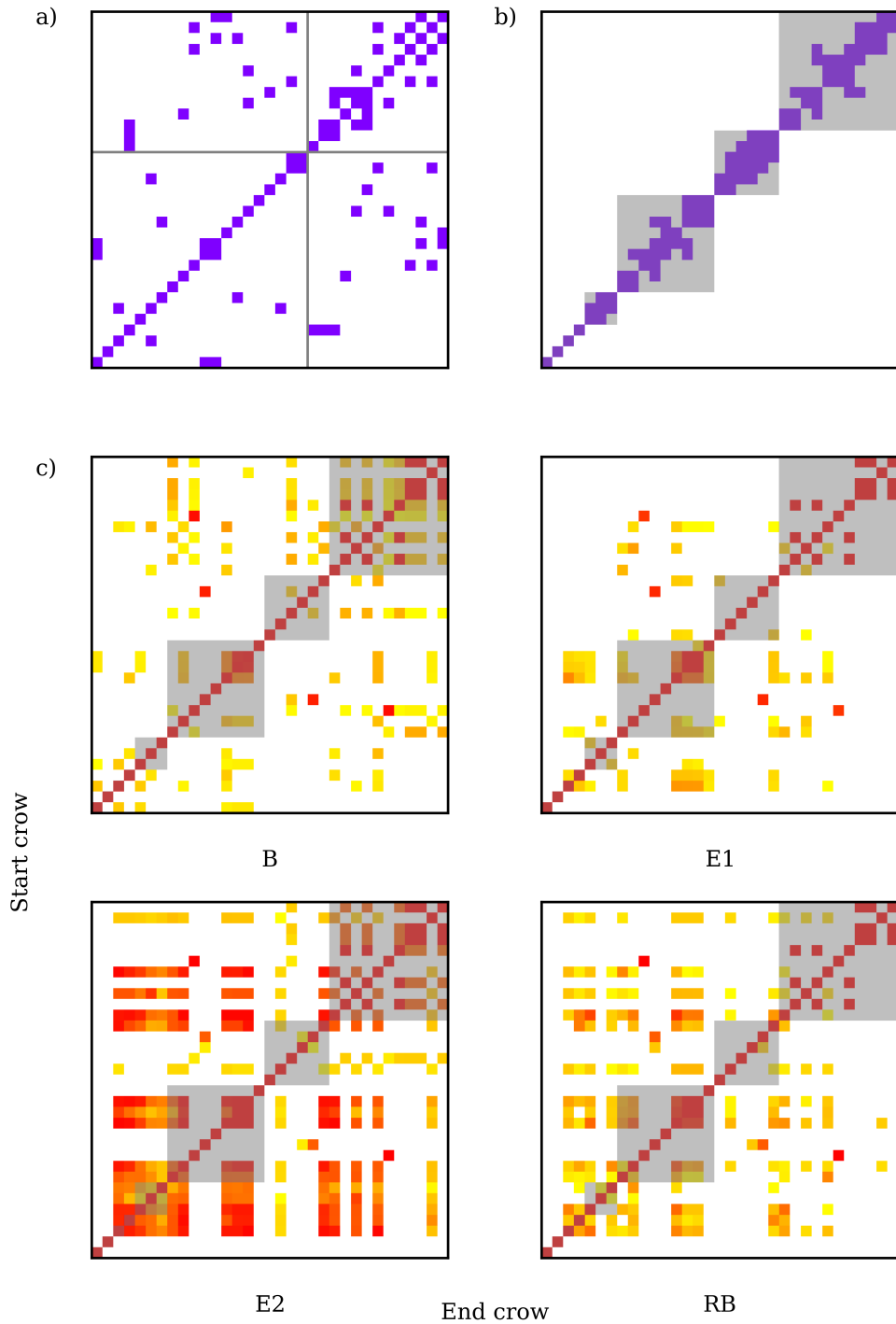


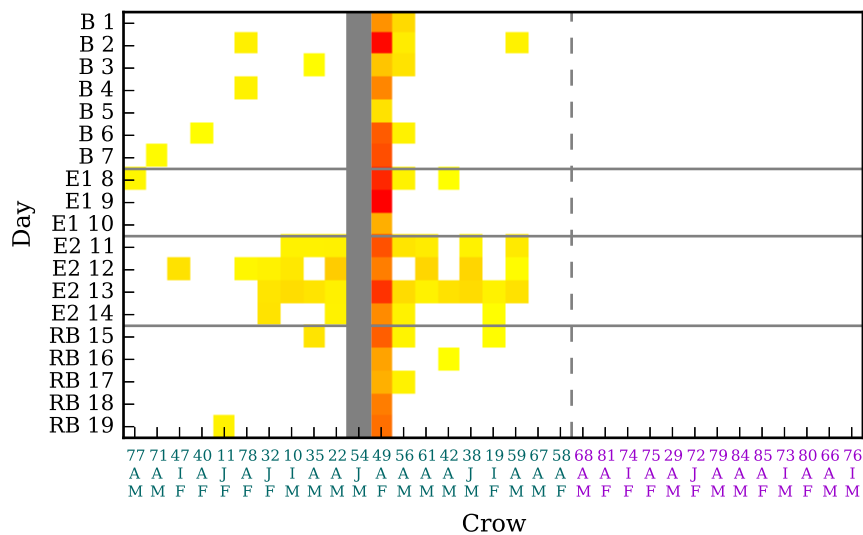
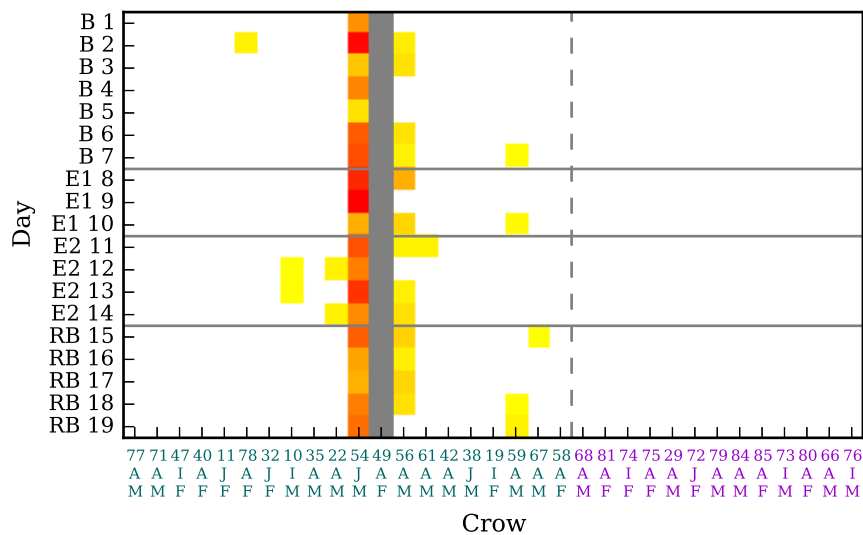
Figure 7.20: a) Matrix showing crows which are first order related shaded in purple. Crows are arranged according to community. b) Crows have been re-ordered into groups in which every crow is first order related to at least one other crow. Groups are indicated by grey shading. c) Emulation results from all four periods with crows ordered according to genetic relatedness.

Figures 7.21c & d show daily encounter durations for crows 56 and 42 respectively. These crows have no first order relations within Magic and neither crow shows a strong preferences for any other crow. Crow 56 was the most gregarious of the crows in the study associating with many other crows on most days. Crow 42 associates with 8 different crows during the B, for an average total duration of 1.5 days each.

To study the temporal paths when information takes longer to transfer ($\lambda > 5 \text{ min}$) emulations need to be run for longer than 1 day to allow the information to spread. This has been achieved by running *multi-day* emulations where the set of informed crows at the end of one day is used to initialise emulations on the subsequent day. In principle multi-day emulations can be run on any combination and order of study days.

Figure 7.22 shows how the size of the outdomain changes with λ for multi-day emulations. In Figure 7.22a multi-day emulations have been run through all 7 days in B. For comparison, Figures 7.22b & c show multi-day emulations which have been run on the same day 7 times. For these I have used the two B days with the largest outdomain, days 1 & 2. 1000 emulations were run with each starting crow and each value of λ and the size of the outdomain was averaged for each combination. Figure 7.22 shows results only for crows in Magic.

Most of the lines in the figures show the outdomain starting out large at small values of λ ($\sim 20 \text{ sec}$) and then dropping off at around $\lambda \approx 5 \text{ min}$ before flattening out at zero at $\lambda \approx 2 \text{ hrs}$. This sigmoidal shape is expected since at small λ time respecting paths exist between most pairs of crows and as λ increases these gradually cease to exist until λ is greater than the maximum total duration of encounters between any pair of crows over the emulation period. The maximum possible outdomain size within Magic during B is 16 as 3 crows in Magic do not have any encounters in this period (see Fig. 7.10a), and Figure 7.22a shows a group of crows for which the size of the outdomain plateaus at just below this maximum before dropping off at $\lambda \approx 5 \text{ min}$. This group of crows all had encounters with crow 56, the most gregarious crow in Magic. The outdomain sizes for the remaining crows do not have such a long plateau and start falling at $\lambda \approx 2 \text{ min}$. This highlights the key role that crow 56 can play in spreading information through the network.



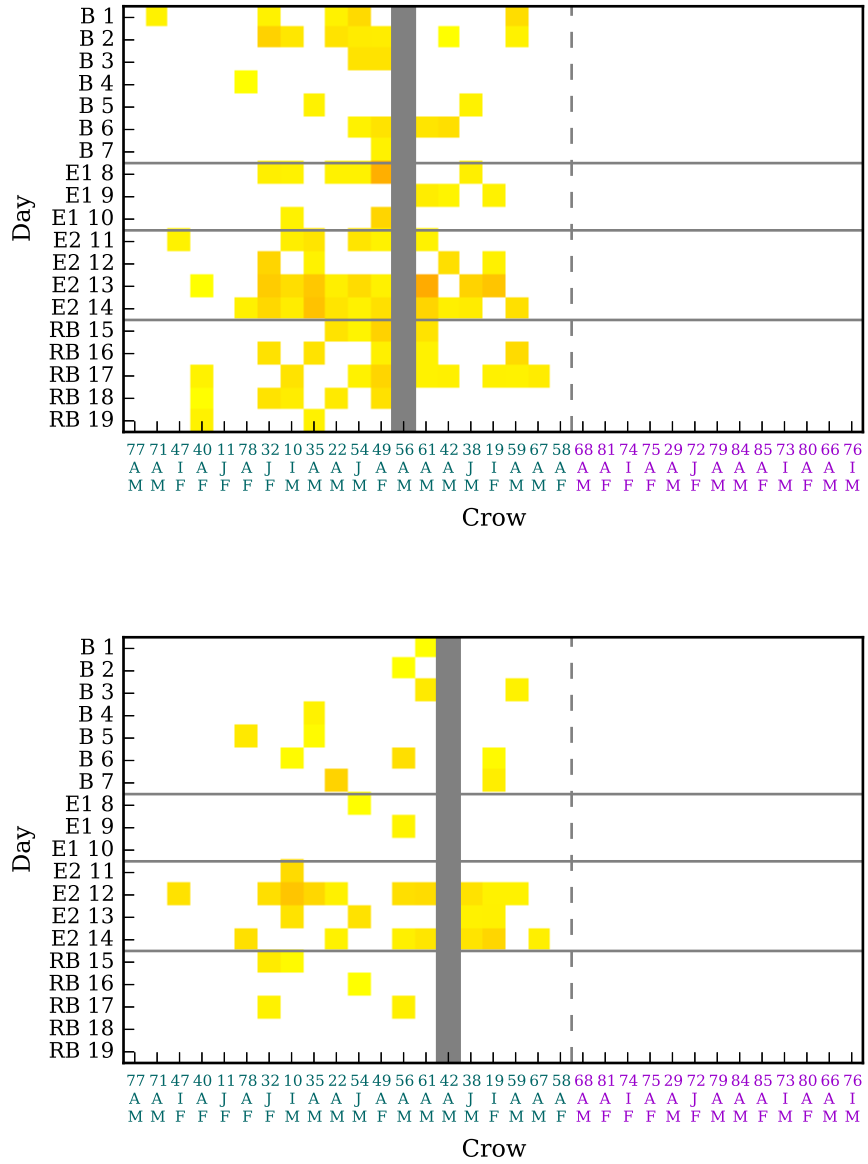


Figure 7.21: Total durations of all encounters with each other crow on each day for a) crow 49, b) crow 54, c) crow 56 and d) crow 42. Crows are ordered according to community.

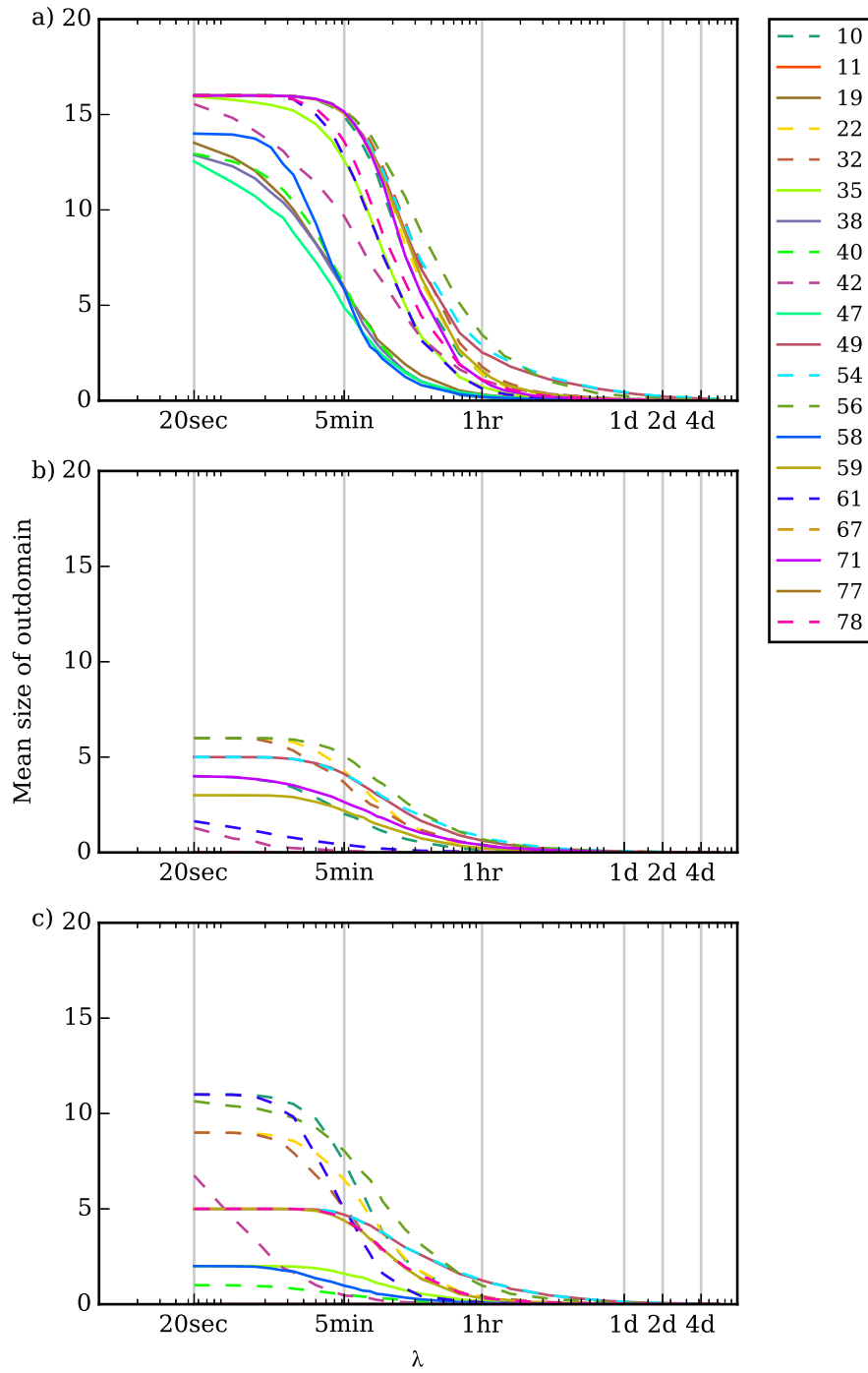


Figure 7.22: Mean outdomain size as a function of λ for multi-day emulations starting with each crow in Magic. a) Emulations have been allowed to run through each of the 7 B days. b) & c) Emulations have been run through the same day 7 times (b) day 1 and c) day 2)

Comparing Figure 7.22a with Figure 7.22b & c shows that the variation in daily networks allows information to spread much further than if all days were the same. The outdomain which results from running emulations through all B days is around 3 times larger than from running emulations through day 1 seven times and twice as large as through day 2.

7.6 Discussion and conclusions

The work in this chapter has analysed the temporal association network of 33 wild NC crows over a period of 19 days. The work has been facilitated by the Encounternet system which allowed automated logging of encounters between animals via animal borne transceivers. This provided a rich dataset of timestamped pairwise inter-crow encounters, including proximity data, from which social networks could be constructed. Such detailed information of crows' associations had previously not been attainable due to the difficulties in observing the birds in their habitat (Rutz et al. 2007).

Static aggregated daily networks revealed two communities within the population which were named Pig and Magic. Pig mainly consisted of strongly associating pairs and triads whereas Magic was more densely connected. Emulations of information flow on daily temporal networks of close range encounters showed that in Pig information was often confined to the pair or triad in which it originated whereas in Magic information often spread further.

Two manipulations were carried out during the study. During E1, a food source (a section of candlenut tree) was placed midway between capture sites Pig and Magic. This produced no noticeable effect on network measures. The second manipulation E2 consisted of placing food sources in the centres of Pig and Magic. Whilst this produced no change in network measures in Pig, a large effect was seen in Magic. An increase in the node degree during E2 resulted in the mean size of the outdomain being 4.1 times larger in E2 than in B. The differences in effect between Magic and Pig could be due to Pig consisting mainly of family groups of three crows whereas in Magic the family groups were not so well defined. It could also be possible that not all the crows in Pig discovered the food source.

Arranging crows into groups where each member was first order related to at least one other member revealed that a large proportion of information pathways were between crows which were members of different groups. This suggests there is potential for information to be passed between family groups. This is an important result in the context of previous NC crow studies as past evidence had favoured vertical information flow over horizontal or oblique (Kenward et al. 2004, Holzhaider et al. 2011).

Temporal analysis of the Encounternet dataset brought with it new challenges. The first problem was to amalgamate reciprocal logs recorded by pairs of tags. Two crows were deemed to be in an encounter during any period where one of their tags received a signal meeting the FC of $\text{RSSI}_{\text{mean}} \geq 15$. This method could have been improved if each of the tags had been tested to ascertain whether there were differences in transmission power. Variation in tag transmission power could cause crows to appear more or less sociable than they really are.

The second challenge was to choose suitable parameter values for the emulations. Results were based on encounters where $\text{RSSI}_{\text{mean}} \geq 15$ which corresponds to distances of up to $\sim 5\text{m}$ (Burns et al. in prep.). This distance was deemed sufficiently close for social learning of tool-oriented behaviours to be plausible. The results are however qualitatively robust to changes in filter level with outdomains reducing slowly and smoothly as the filter level is lowered. The effects of E2 are visible from filter levels of $\text{RSSI}_{\text{mean}} \geq 10$ upwards.

Emulations were also run using the parameter λ , the mean time for information to transfer, set to 5 min. Although this choice was arbitrary 5 min was thought to be a reasonable time period to allow one crow to observe the foraging behaviour of another, a minimum requirement for social learning to occur. It also happened to be a suitable period to allow potential information pathways through the network during one day to be differentiated in terms of probability.

Finally having run the emulations there was no established method of analysing the results. Different metrics for measuring information flow were trialled before settling on outdomain. These included ‘time taken to inform n other crows’ and latency (see Sec. 2.3). Outdomain was chosen because it was the most direct way of quantifying the results of the emulations. The stochastic variation in λ gave variation in outdomain allowing the relative probabilities of different information

pathways to be assessed. Matrix plots allowed the full range of outdomain to be shown whilst avoiding taking averages over crows which can hide interesting features in the results.

This study is part of a small but growing number of animal studies which with the aid of technologies such as Sirtrack and Encounternet are collecting temporal association data. Some studies are exploratory, seeking to determine the capabilities of the technologies in the field and recommend best practice (e.g. Mennill et al. 2012). Other studies use the technologies to gather timestamped data but then aggregate the data before analysing. One example of this is Böhm et al. (2009) which studied contacts between badgers (*Meles meles*) and cattle to study the spread of bovine tuberculosis in Britain. They aggregated contact data to give the number and total duration of contacts per day for each collared badger and cow in an effort to gauge inter and intra-species contacts. In a similar study, Ji et al. (2005) recorded proximity data between brushtail possums (*Trichosurus vulpecula*) in New Zealand also aiming to understand the spread of bovine tuberculosis. Ji et al. looked at the distribution of contact rates from month to month over the 3 years of the study.

Whilst other ASN studies have analysed the flow of information (or disease) through the network, most play out an SI or related model on a static network. An exception to this is Blonder and Dornhaus (2011) which investigated the potential flow of information through colonies of ants (*Temnothorax rugatulus*). They gathered time-stamped interaction data through video recording the ants. They then emulated the potential flow of information on the empirical data set. Their emulation is slightly different to the one performed in this chapter as their network is, in the terminology of Holme and Saramäki (2012), a contact series – a series of instantaneous contacts, whereas the crows network is an interval graph meaning the encounters between crows had a finite duration. Blonder and Dornhaus compared their emulations to information flow predicted by a kinetic gas diffusion model of a colony and found that information flow on the empirical data was significantly slower.

One notable example which partially embraces temporal networks is Hamede et al. (2012) which simulated the spread of devil facial tumour disease (DFTD) through the Tasmanian devil (*Sarcophilus harrisii*) population. DFTD is an infectious cancer which threatens the Tasmanian devil population with extinction

(Hamede et al. 2009). Using Sirtrack collars encounters between 46 adult devils were logged over a period of 5 months. The chosen months spanned both the mating and non-mating seasons so that the differences could be assessed. Dynamic populations of adults were simulated in which new nodes were added at regular time intervals to represent juveniles reaching maturity. The social network was generated randomly with ratios of edges between and within sexes matching the observed population. A Susceptible-Exposed-Infected (SEI) model was then played out on the random networks with the networks being re-wired at regular intervals to represent the transitions from mating to non-mating seasons. They use their model to predict the probability of extinction.

Although Hamede et al. (2012) does not use a fully temporal network where edges exist only during devil encounters, they have considered the changes in network topology that arise between the mating and non-mating seasons and their otherwise static network is re-wired twice a year to reflect this. They ran simulations as opposed to emulations as their infection model was played out on artificially created networks as opposed to real data. Whilst their results could have more closely represented disease dynamics in the 46 collared devils by incorporating the timings of encounters, this may not have been useful for their purpose as they wished to draw conclusions relevant to the entire Tasmanian devil population. They also drew conclusions over a far longer time frame than the periodicity of encounters so the time ordering could be less important.

Other studies have used Network Based Diffusion Analysis (NBDA) (Sec. 3.3.3) to analyse the spread of information through an ASN (e.g. Kendal et al. 2010, Atton et al. 2012, Aplin et al. 2012, Allen et al. 2013). In addition to determining the social network of the population, these studies require knowledge of the order in which individuals become informed. Aplin et al. (2012) investigates the spread of knowledge of new food sites amongst blue tits (*Cyanistes caeruleus*), great tits (*Parus major*) and marsh tits (*Poecile palustris*). The social network was inferred from associations where tits visited feeders within 30s of each other. The order of arrival of tits at new food sites was recorded and used to inform models of information spreading. Allen et al. (2013) investigated the spread of a foraging innovation, lobtail feeding, through a population of humpback whales (*Megaptera novaeangliae*).

These NBDA studies use observational data on real learning processes to calculate

the likelihood of social learning or the relationship between the order of learning and the social network. In our study this was not possible as we did not have evidence of actual information transfer. Although we had a rich data set we did not have any information on what the crows were doing during the encounters and so we did not know if actual information was being transferred. This could be the work of a future study which would require the use of bird mounted video cameras (see Rutz et al. 2007 for an example).

Naug (2008) used video cameras to record honeybees returning to a hive with food. From this he was able to track transmission pathways of food being transferred from bee to bee. The transmission pathways were themselves studied as weighted, directed networks. Orally transmitted pathogens can be transmitted via mouth-to-mouth food exchange and so studying these transmission pathways can give insights into how disease may spread through the colony.

This chapter also compared emulations run on temporal encounter data with emulations on an equivalent static network. To my knowledge this is the first ASN study to have done this with empirical data. Daily static networks were constructed by accumulating the durations of encounters between each pair of crows throughout the day and weighting edges accordingly. When running an SI model on the static network the probability per second of information being transferred along a given edge was scaled so that the total probability of transmission over the day was equal to that in the temporal network. On most B days, information spread further in the static network than in the temporal one illustrating the fact that studies emulating information flow on time aggregated networks run the risk of overestimating the speed and extent of the flow. The difference in the results is due to the time ordering of encounters in the temporal network. Information must flow along time respecting paths (see Sec. 2.3) and this significantly reduces the number of ways that information can pass through the network.

SI models were also run on static networks in Voelkl and Noë (2010). This study aimed to identify features of network topography which affected propagation speed. Social networks were constructed based on empirical interaction data relating to 70 primate groups from a range of 30 species including lemurs, monkeys and apes. SI models were played out on four different types of network. Firstly a weighted graph of empirical data, secondly a binary graph made from the empirical data, thirdly an edge randomisation of the empirical network preserving

edge weights, and lastly a fully connected binary graph. They found the weighted empirical graph to have the slowest propagation speed and the fully connected graph to be the fastest. Voelkl and Noë (2010) did not however have access to temporal data and so was unable to test their findings.

In summary this chapter has investigated the potential for information flow through a population of NC crows. Having access to timestamped proximity data has allowed information flow to be emulated on a temporal network which is more realistic than relying on static network data.

Part IV

Conclusions

Chapter 8

Conclusions

This thesis has focussed on two different approaches for analysing ASNs. Part II was based on a study of Trinidadian guppies (*Poecilia reticulata*) in which observations of group membership were used to infer association. Manual observations from 12 censuses yielded a sparse dataset and were accumulated to construct a single static network giving a ‘snapshot’ of the guppies’ social structure. In contrast in Part III a temporal network of New Caledonian crows (*Corvus moneduloides*) was constructed from timestamped proximity data collected over a 19 day period. The collection of this dataset was automated and continuous during daylight hours.

Analysis of the guppy social network (Ch. 5) found persistent pairwise associations which are a prerequisite for co-operative behaviour (Croft et al. 2004b). The main aim of the study was to determine if relatedness is a factor contributing to the social structure. No evidence for this was found, which is an interesting result when viewed in the context of co-operative behaviour. In this study the argument of inclusive fitness does not appear to explain the social preferences of the guppies and so the question of what mechanisms drive the social structure still remains. Associations between male guppies were also investigated to see if these are influenced by body colourings. This study found evidence suggesting that colour could indeed play a role.

The following chapter (Ch. 6) tests association indices (AIs) in the scenario of an open population where animals can leave the study area. This was done using

simulated data for an idealised model for which a maximum likelihood estimator (MLE) was also derived. The MLE performed the best on the simulated data. Networks constructed from the guppy data using SRI and HWI were compared. When edges were ranked by association strength the rankings given by the two indices had large differences such that conclusions drawn from the two networks could differ. There remains much work to be done to improve the selection of the most appropriate AI for each study. The work in Ch. 6 could also be customised to suit other sampling scenarios as each study species has different biases which must be considered on a case by case basis.

The crow dataset (Ch. 7) provided a second by second account of inter-crow encounters throughout the study. This meant that differences in behaviour could be seen between different periods of the day and between different days of the study. Information flow through the network was emulated to assess the potential for information to spread through the network. The emulations showed that the connectivity of the network was high enough to allow information to spread on average to 6 other crows during one day. Taken together with relatedness analyses which revealed that a large proportion of information pathways connect crows that are not first order related, this suggests there is the possibility for tool use skills to be learned socially.

The automated collection of crow proximity data was made possible by new advances in technology. A variety of technologies including PIT tags, RFID and transceivers have recently become practical options for gathering data for ASN studies (Krause et al. 2013). Principally, devices have been manufactured smaller and lighter enabling them to be attached to many species of animals. The NC crow study made use of transceivers which were fitted to the crows using detachable back packs. The transceivers logged inter-crow encounters recording the time, duration and signal strength for each log. Manual collection of this dataset would have been impossible not just because of the quantity of data obtained but also because NC crows are just too difficult to observe. The dense rainforest in which they live combined with the tendency of crows to remain hidden makes observation challenging. For the crow system, transceiver technology has opened up many possibilities for future studies.

Although new technologies are exciting they bring with them two new sets of problems. Firstly there are challenges in data processing. Encounters between

pairs of crows are recorded twice, once by each crow's transceiver, and these records must be amalgamated to produce a single unified account of the encounters. The relationship between signal strength and distance must also be determined and decisions made about which distances are meaningful and should be included in the study. Secondly, access to temporal data raises many questions about how best they should be analysed. Until now relatively few ASN studies have used temporal networks and so analysis methods are still in their infancy. New ways must be found to visualise data and suitable metrics established to quantify the structure.

It is clear that advances in technology have opened up many possibilities for new areas of study through the collection of rich and large datasets. However there are still many situations in which automated data collection techniques cannot be used. The guppy is an example of a species too small for the use of physical tags. In addition pools in Trinidad are too large to film or photograph so manual collection of data remains the only viable option. Temporal network analysis is an exciting new technique for behavioural ecology but there remain many cases in which static network analysis is sufficient. If the research question, such as assortment by relatedness of the guppy network, does not involve dynamics of the network or processes on the network then static network analysis is still a powerful tool for uncovering new biology. There are still valuable lessons to be learnt from systems such as the guppies and therefore developing analysis methods for sparse datasets and static networks, such as the work discussed in Chapter 6, remains important.

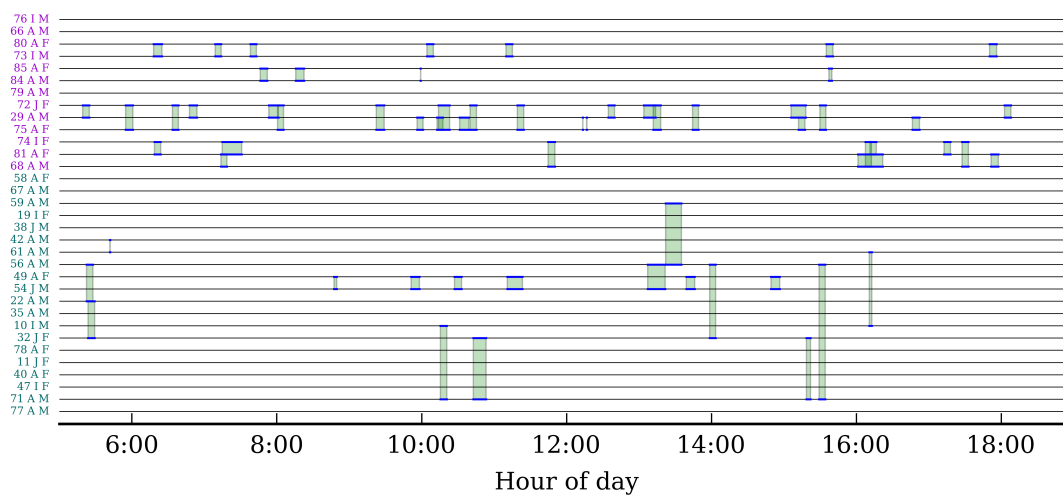
Part V

Appendices

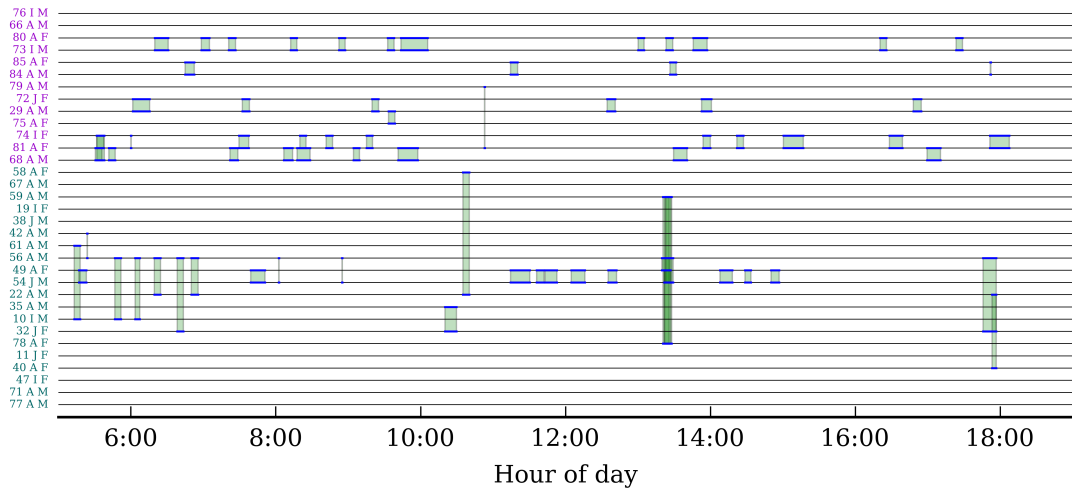
Appendix A

Crow encounters

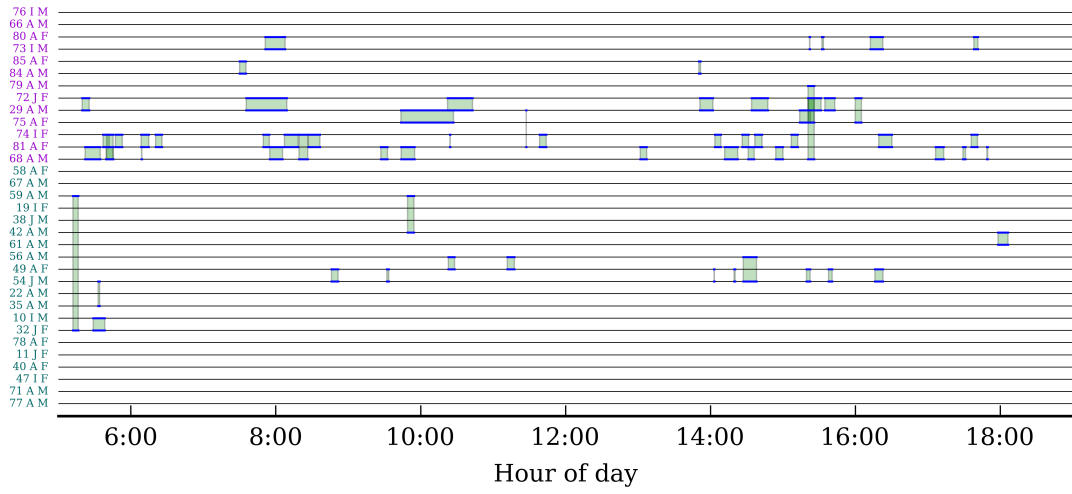
In this appendix I display data from the New Caledonian crow study (Ch. 7). I show a timeline plot for each study day in order to show their similarities and differences. The encounters have been filtered to have $RSSI_{\text{mean}} \geq 15$ and have been amalgamated as described in Section 7.3.1. All emulations were conducted on these data.



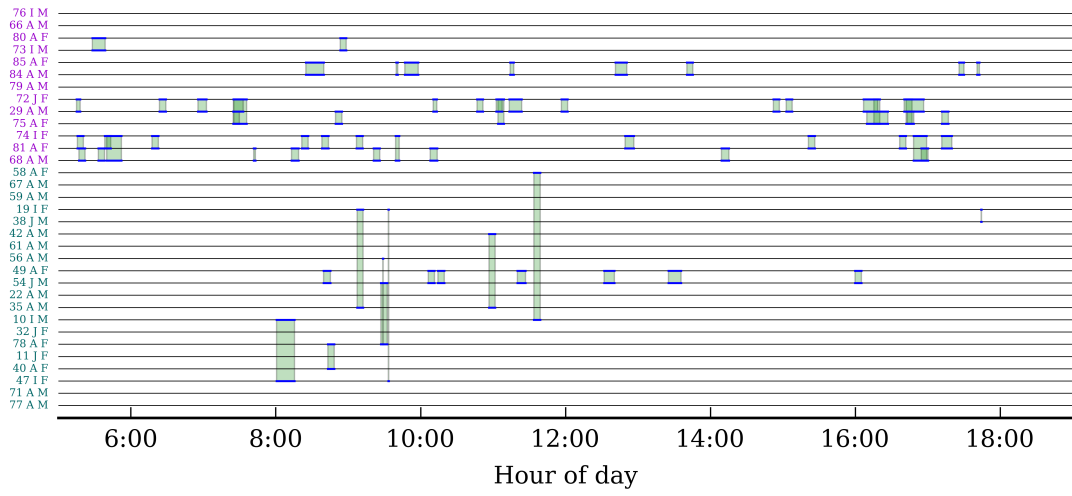
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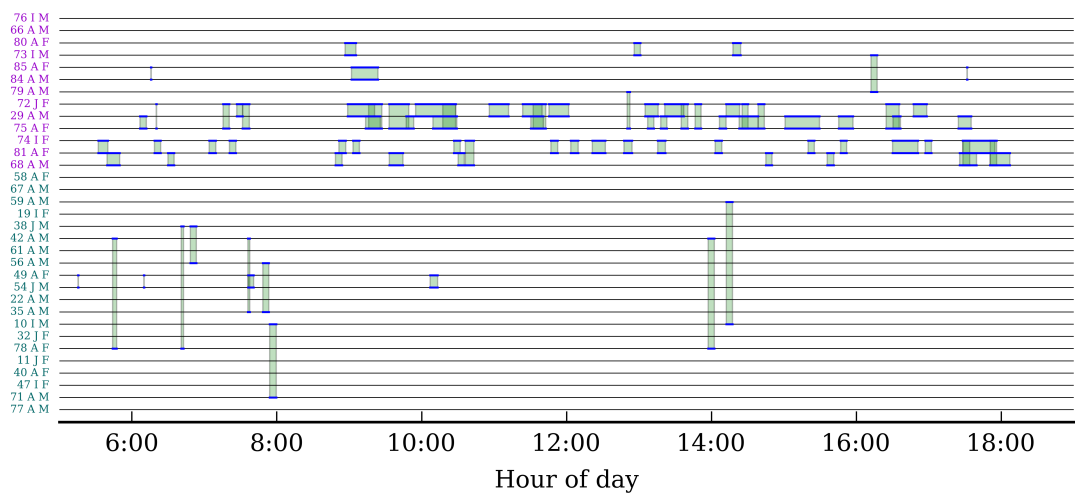
B: day 2



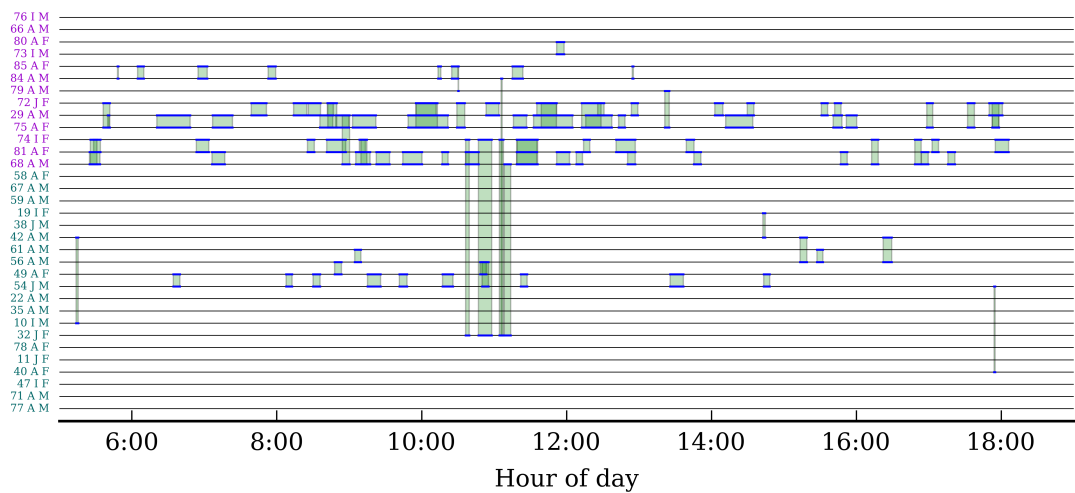
B: day 3



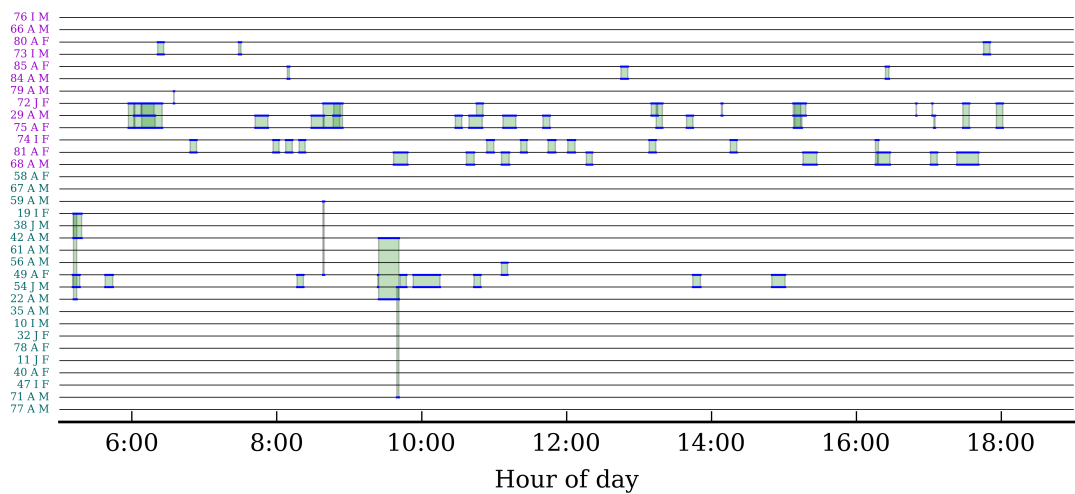
B: day 4



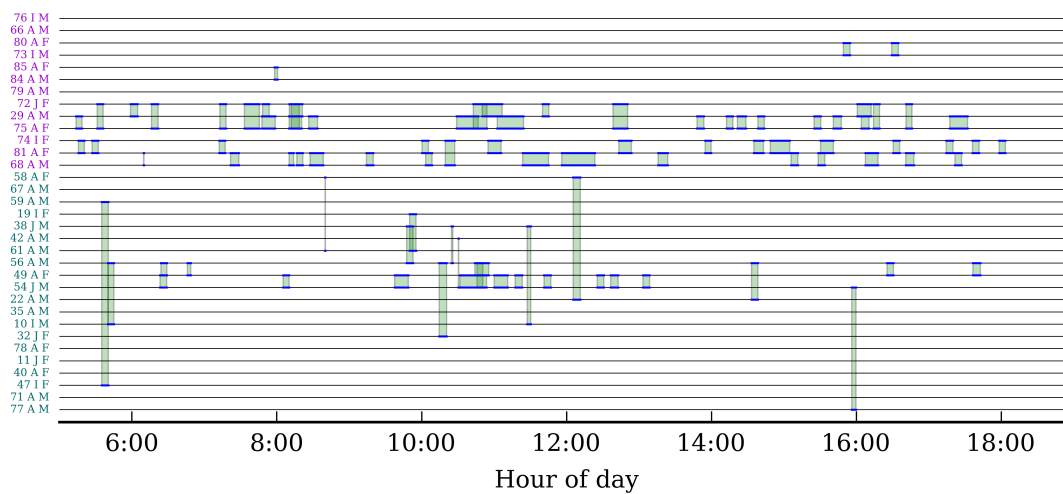
B: day 5



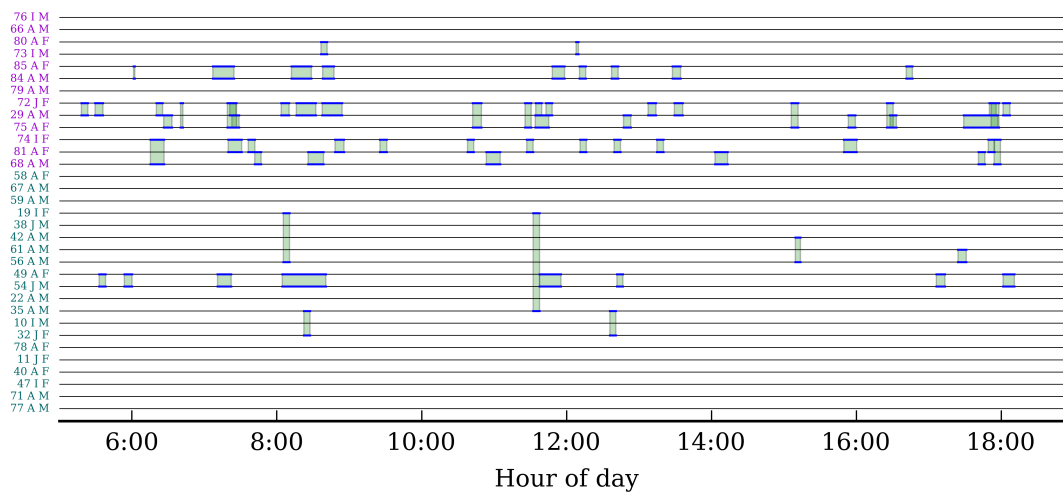
B: day 6



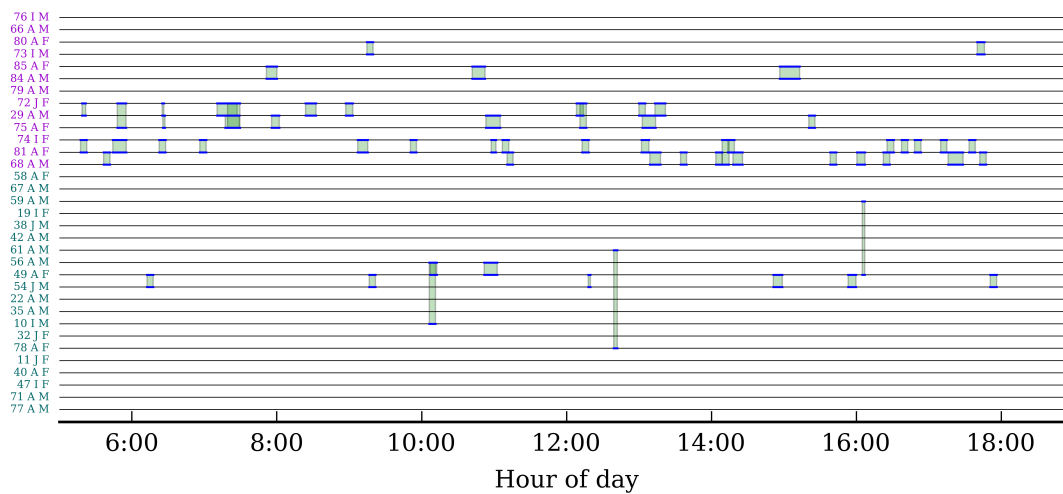
B: day 7



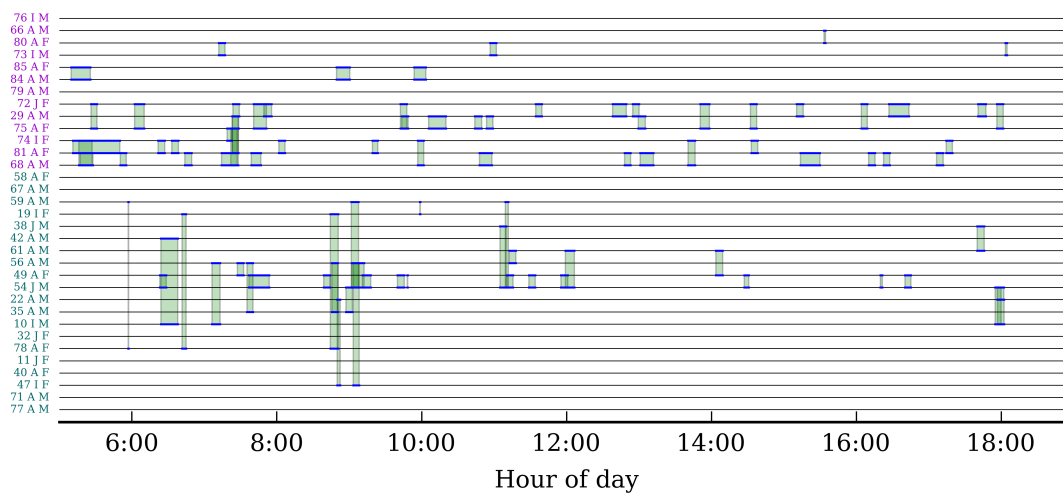
E1: day 8



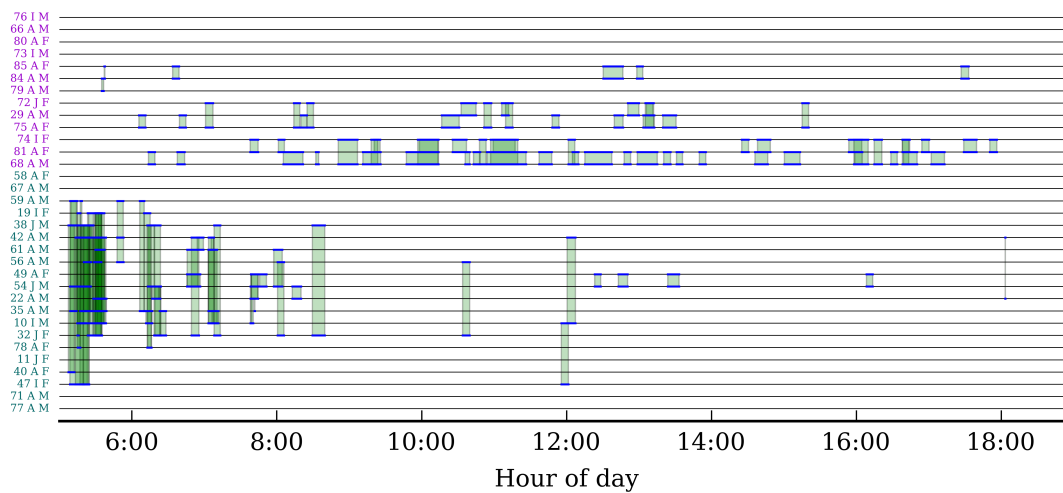
E1: day 9



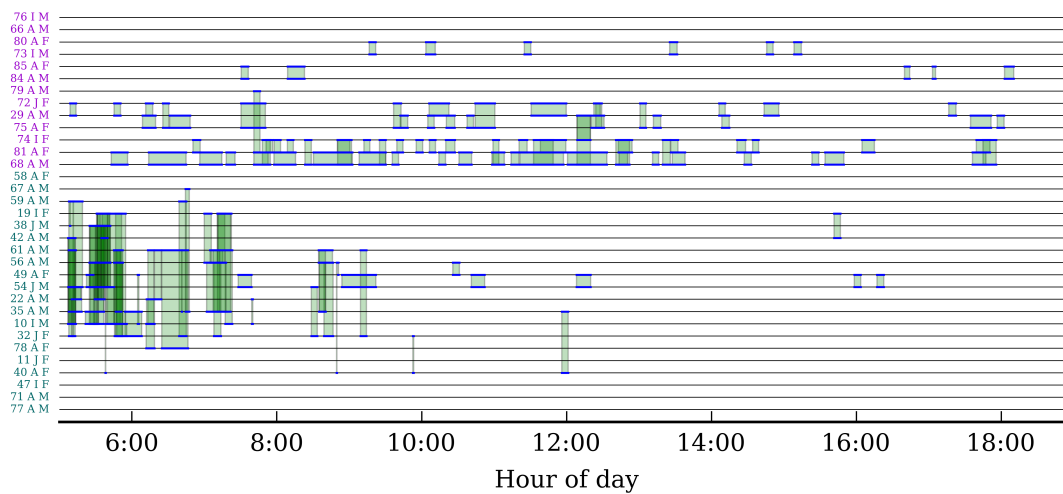
E1: day 10



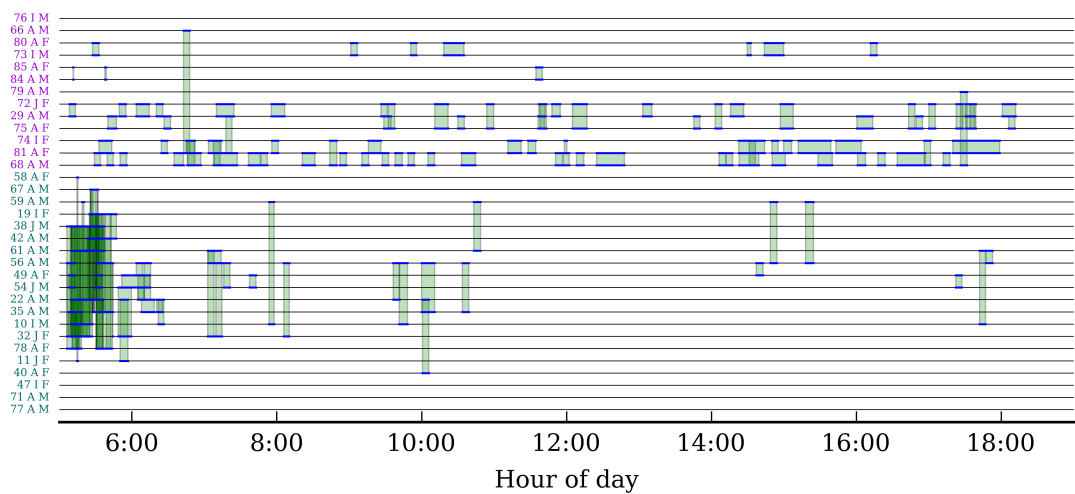
E2: day 11



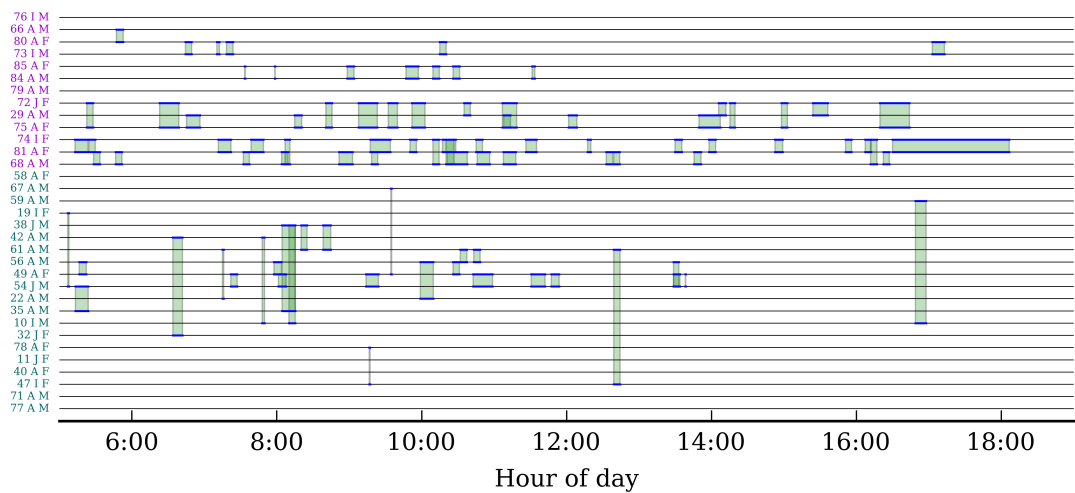
E2: day 12



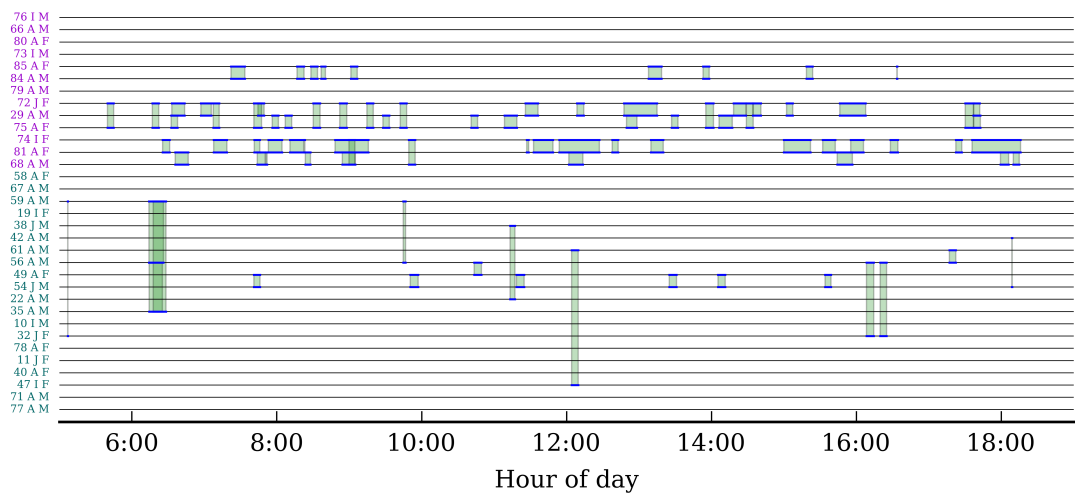
E2: day 13



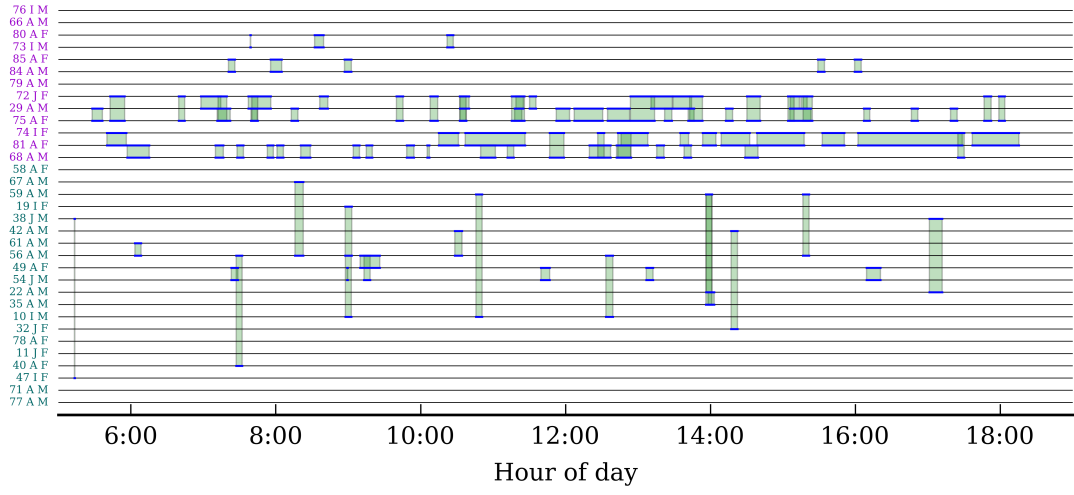
E2: day 14



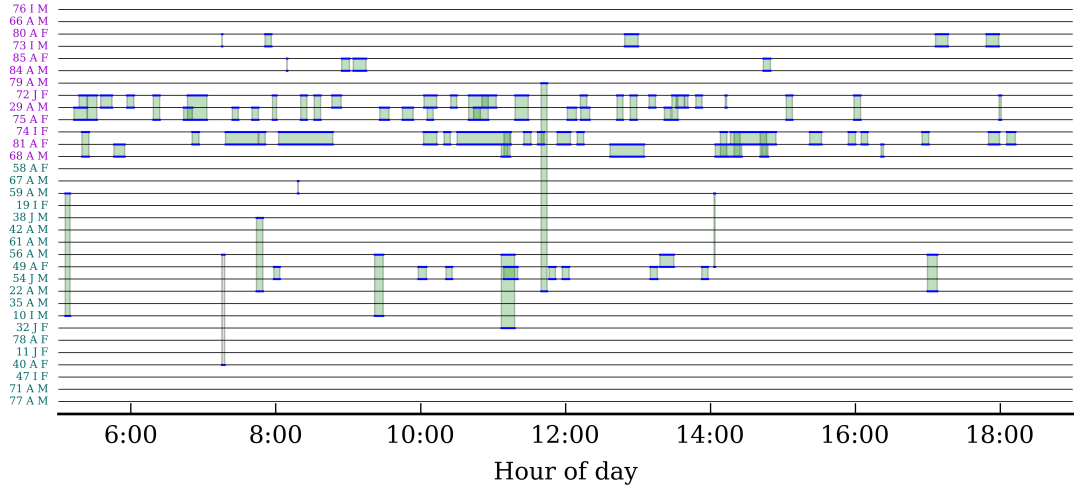
RB: day 15



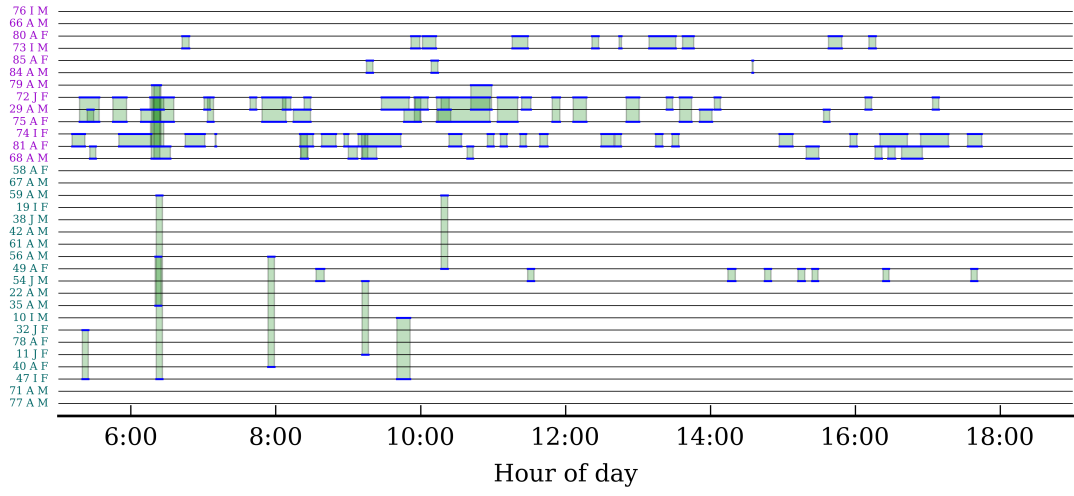
RB: day 16



RB: day 17



RB: day 18



RB: day 19

Figure A.1: Timeline plots of all encounters having $RSSI_{mean} \geq 15$ on each study day.

Appendix B

Data management, algorithms and packages used for this thesis

Analyses of the Trinidadian guppy and New Caledonian crow datasets were executed in Python, a high level programming language. Python is particularly suited to scientific computing as it can be written quickly which is beneficial as coding objectives in scientific research change frequently. There is also a wealth of packages available to aid computations. For this thesis I have made extensive use of NumPy and SciPy packages (Jones et al. 2001) which provide tools for linear algebra and statistics. Most figures have been made using the matplotlib package (Hunter 2007) which has proved to be extremely versatile for visualising data.

For conceptualising networks I used the igraph package (Csardi and Nepusz 2006) which has a Python implementation. igraph lets the user create a graph object and keep track of nodes and edges as they are added or removed from the network. igraph contains many useful functions for generating and manipulating graphs and assigning attributes to nodes and edges. It also implements algorithms for many common network problems such as calculating the degree distribution or finding the shortest path between two nodes. Furthermore igraph provides classes for visualisation of the network. All the network diagrams in this thesis were made using igraph.

MySQL databases were used to store the datasets for both the guppies and the

crows. The Python code accessed the databases directly allowing large datasets to be imported conveniently. The versatility of sql meant that some initial data processing could be delegated to the MySQL server which was faster than implementing the processing in Python.

B.1 Emulating information flow on a temporal network

The New Caledonian crow dataset consists of a collection of time-stamped pairwise encounters between crows (Ch. 7). Each line of data contains two crow I.D.s, a start time, an end time and a duration (equal to the difference between start and end times). Analysis of this dataset involved emulation of a hypothetical piece of information through the network (Sec. 7.4). This section describes the algorithm used to perform the emulation.

Emulation of information flow on a temporal network is an example of discrete event simulation (DES). In this process the system can be modelled as a series of events where each event happens at an instantaneous moment in time (Banks and Carson 1984). Each event changes the state of the system but between events the system remains unchanged (Banks and Carson 1984). For my research I have defined three types of events, ‘start’, ‘end’ and ‘transmission’. A start-event happens when an encounter begins between two crows A and B . At this point in time, an edge is added to the network between nodes A and B . An end-event happens when an encounter between crows A and B ends. At this point in time, the edge between nodes A and B is removed from the network. The remaining transmission-event occurs when an uninformed crow becomes informed. At this point the node attribute for the recipient crow can be updated to reflect its new state.

A useful consequence of DES is that a simulation can run in *event-time*, meaning that the simulation can jump sequentially from one event to the next without having to consider the time in between. A good way of implementing this is to store all events in a data structure called a *heap* (implemented in the Python package `heapq`). A heap is a binary-tree data structure in which the value of a key k (in this case the event time) for each node is less than or equal to the

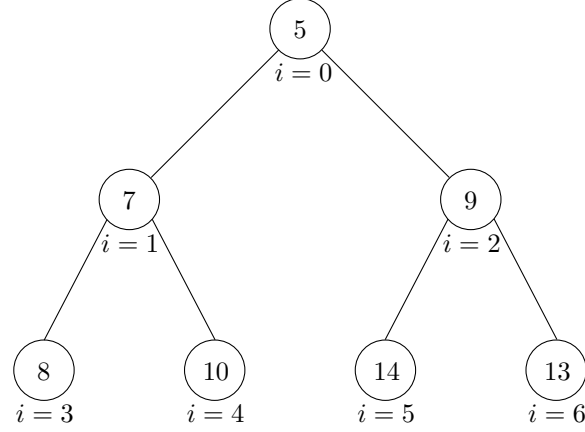


Figure B.1: Example of data organised in a heap H . $H[0]$ is always the smallest element and $H[i] \leq H[2i + 1]$ and $H[i] \leq H[2i + 2]$ for all i .

value of k for either of the node's two children (Fig. B.1). This is called the heap invariant. The root of the heap has the smallest value of k . The time taken to sort data using this structure is of order $n \log n$. Use of a heap allows the first event (the event with the smallest event time) to be removed from the heap using the *pop* function. The heap will then be adjusted to maintain the heap invariant. Adding additional events to the heap, an operations which will be used multiple times to emulate information flow, can be done very quickly.

The algorithm used for the emulation is shown in Algorithm 1. The procedure takes two parameters, the start node for the emulation and the day on which to run the emulation. A graph object is created to keep track of the changes in the network. Initially there are no edges in the network and all nodes apart from the start node are set to 'uninformed'. The running time of the algorithm is dependent on the number of events in the heap and so only events which could be used for the emulation are added to the heap. Transmission-events are conditional upon one crow of a pair being uninformed and so only events involving a single informed crow are added to the heap. Initially all start and end-events involving the start crow are returned from the database and added to the heap.

The main component of the algorithm steps through all events in the heap until the heap is empty. Different actions are performed depending on the type of each event. Events contain the node I.D.s of the crows involved as well as the event time and type. Start-events also contain the duration of the encounter. If the current event is a start-event, an edge is added to the network between the two nodes *node1* and *node2*. The presence of an edge indicates the start

of an encounter in which transmission of information from the informed to the uninformed crow may take place. If transmission occurs, it will happen at some time t in the future which can be calculated using the process described in Section 7.4.1. The function ‘getTransmissionEvent’ is used to calculate t and return a transmission-event. If the waiting time until t is less than the duration of the encounter the transmission-event is added to the heap. If the current event is an end-event the edge indicated by the event is removed from the network.

In a transmission-event, the node I.D.s are ordered such that the direction of transmission of information is implied from $node1 \rightarrow node2$. If the current event is a transmission-event it is first necessary to check that $node2$ is not already informed as information may have already reached it via an alternative path. If $node2$ is not already informed, the transmission process is carried out by setting $node2$ to be informed and recording this transmission in the emulation path list. As there is now a newly informed node in the network, all start and end-events involving this node must now be returned from the database and added to the event heap.

B.2 Emulating information flow on an equivalent static network

Chapter 7 also requires emulations of information flow to be carried out on a static network. The static network is created by aggregating all encounters on one day. Edges exist between pairs of crows which had at least one encounter during the day. Edges are weighted by the mean time taken for information transfer λ'_{AB} as calculated in Section 7.4.4.

As with the temporal network case the emulation can be modelled using DES, but the algorithm is simplified (Algorithm 2). As edges are present throughout the day, there is now just one type of event – a transmission-event. The first step is to cycle through each edge connected to the starting node and calculate a transmission time for a transmission-event on each edge. These transmission-events are then added to the heap.

Stepping through each event in the heap is now much simpler. For each event,

Algorithm 1 Emulation of information flow on a temporal network on day d starting with node n

```

1: procedure RUNEMULATION( $n, d$ )
2:    $DB \leftarrow \text{DATABASE}$  ▷ Link to database containing all events
3:    $G \leftarrow \text{GRAPH}$  ▷ Initialise a graph object
4:    $H \leftarrow \text{HEAP}$  ▷ Initialise a heap object
5:    $P \leftarrow \text{LIST}$  ▷ List in which to store emulation path
6:
7:    $events \leftarrow DB.\text{GETEVENTS}(n, d)$  ▷ Get all events involving node  $n$  on day  $d$ 
8:    $H.\text{ADD}(events)$  ▷ Add all events to the heap
9:
10:  Set  $G[n].informed = \text{True}$ 
11:
12:  while  $\text{length}(H) > 0$  do
13:     $E \leftarrow H.\text{POP}$  ▷ Remove the first event in the heap
14:     $event\_time \leftarrow E.event\_time$ 
15:     $event\_type \leftarrow E.event\_type$ 
16:     $node1 \leftarrow E.node1$ 
17:     $node2 \leftarrow E.node2$ 
18:
19:    if  $event\_type = \text{"start"}$  then
20:       $G.\text{ADDEDGE}(node1, node2)$ 
21:       $E\_trans = \text{GETTRANSMISSIONEVENT}(E)$ 
22:       $H.\text{ADD}(E\_trans)$ 
23:
24:    else if  $event\_type = \text{"end"}$  then
25:       $G.\text{REMOVEEDGE}(node1, node2)$ 
26:
27:    else if  $event\_type = \text{"transmission"}$  then
28:      if  $G[node2].informed = \text{False}$  then
29:        Set  $G[node2].informed = \text{True}$ 
30:         $P.\text{APPEND}(node1, node2, event\_time)$ 
31:         $events \leftarrow DB.\text{GETEVENTS}(node2, d)$ 
32:         $H.\text{ADD}(events)$ 
33:      end if
34:    end if
35:  end while
36:  return  $P$ 
37: end procedure

```

check that the intended recipient node ($node2$) is still uninformed. If it is, then proceed to set $node2$ to be informed and calculate transmission-event times on all edges connecting $node2$ to an uninformed node.

Algorithm 2 Emulation of information flow on a static network on day d starting with node n

```

1: procedure RUNEMULATION( $n, d$ )
2:    $G \leftarrow \text{GRAPH}$                                 ▷ Initialise a graph object
3:    $H \leftarrow \text{HEAP}$                                 ▷ Initialise a heap object
4:    $P \leftarrow \text{LIST}$                                 ▷ List in which to store emulation path
5:
6:   RUNINFECTEDNODE( $n, H, P$ )
7:
8:   while length( $H$ ) > 0 do
9:      $E \leftarrow H.\text{POP}$                                 ▷ Obtain the earliest event in the heap
10:     $node2 \leftarrow E.node2$ 
11:
12:    if  $G[node2].informed = \text{False}$  then
13:      RUNINFECTEDNODE( $node2, H, P$ )
14:    end if
15:  end while
16:  return  $P$ 
17: end procedure
18:
19: function RUNINFECTEDNODE( $n, H, P$ )
20:   Set  $G[n].informed = \text{True}$ 
21:
22:   for all edges connected to  $n$  do
23:      $E \leftarrow \text{GETTRANSMISSIONEVENT}(n, edge)$ 
24:     if  $E.event\_time$  is before sunset then
25:        $H.ADD(E)$ 
26:     end if
27:   end for
28: end function

```

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